Distribution, Spawning and Racial Studies of the Capelin, *Mallotus villosus* (Müller), in the Offshore Newfoundland Area[1,2]

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ABSTRACT

It was definitely established in July, 1950, that capelin were spawning on the Grand Bank. Samples of spawn taken in 1950 on the Southeast Shoal of the Grand Bank indicate that capelin were spawning in temperatures as low as 2.8°C. In 1951 spawning temperatures were some two degrees higher. These temperatures are 2 to 4°C. lower than those reported for beach spawning. Capelin, apparently, also spawn on other areas of the bank. The effects of low temperature in 1950 resulted in spawning taking place in the middle of July and the subsequent slow incubation of the eggs would result in larvae being liberated late in September. In 1951 capelin spawning, in the same area of the Grand Bank, took place around the latter part of June or the first of July and larval liberation around the first of August.

Meristic studies using vertebral counts indicate that except for the 1950 year-class there is no real difference between any group from Grand Bank areas. The over-all averages for all years from the Grand Bank do not differ significantly from those found inshore by Templeman (1948).

Up to the time of spawning the male capelin were found to be the more numerous.

INTRODUCTION

In the Newfoundland area capelin and cod are probably the most abundant fishes. In spite of their great and widespread abundance in the area, capelin are close to the coast for a brief period of the year only, and are not strictly considered to be a commercial fish. Their familiarity along the coast can perhaps be attributed to the manner in which they make their appearance and the magnitude of the population. In June and early July capelin approach the coast in very large schools and when suitable conditions prevail mass spawning takes place on or near the beach. At the height of the spawning activity the beach becomes "alive" with the squirming fish as each wave brings them in, and then recedes leaving thousands stranded on the beach.

In 1950 the presence of a spawning population of capelin was observed on the Southeast Shoal of the Grand Bank. Although it was known that capelin spawn in deep water near the coast this was the first time that it was known that capelin also spawn on the Grand Bank.

Figure 1 is a photograph of a mature male and a mature female capelin taken during the spawning period. The male is somewhat larger and much firmer

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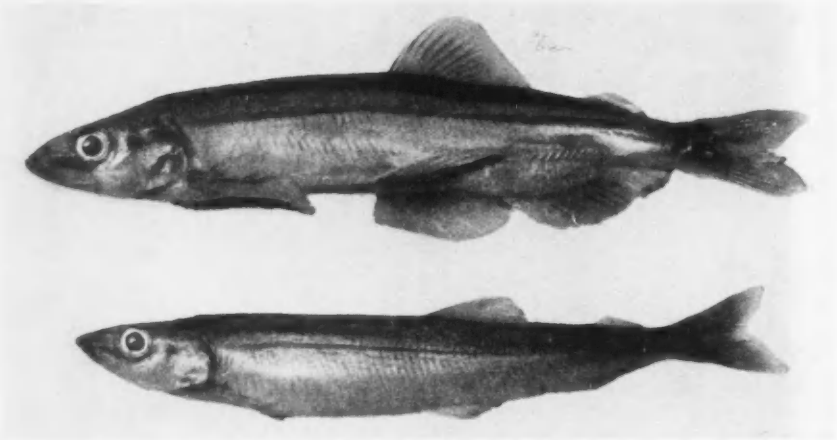

FIG. 1. Mature male capelin (above), female capelin (below) taken during the spawning season. The upper lateral ridge of the male shows as a grey band below the dark dorsal surface, and is bounded below by a narrow dark stripe.

than the female. The pronounced ridges along the sides of the body of the male are described in detail by Templeman (1948). Other obvious differences are the enlarged anal, pectoral and pelvic fins of the mature male. The female is a much more delicate fish and has a more silvery appearance.

Previous work on the capelin by Jeffers (1931), Sleggs (1933), and Templeman (1948) was carried out on specimens taken on the beach or from waters adjacent to the coast of Newfoundland. The latter paper in particular gives a very detailed account of the inshore spawning population and served as a basis of comparison for the groups studied in this investigation.

ECONOMIC IMPORTANCE

The chief economic importance of capelin is as a food for other fish; for example, it makes up a great share of the diet of cod both inshore and in bank areas. Inshore the large trap fishery for cod is directly dependent on the cod which follow the migrating capelin towards the coast. Other commercial species such as haddock and salmon to a lesser extent also utilize capelin as part of their diet. Capelin also form part of the food of seals, whales and sea-birds.

Capelin are used by man as bait for cod, as fertilizer, are eaten locally and are exported in comparatively small quantities in the fresh, frozen, salted and smoked condition. They are also used as food for dogs and mink and in the preparation of pet food. In recent years capelin have been used in the production of fish meal and oil in order to extend the operations of herring meal plants for several weeks when herring become unavailable. In 1950 about 3,000,000 lb. (1,400,000 kg.) of meal were produced from capelin, in 1952 the production fell to 188,000 lb. (85,000 kg.), but since this time none has been produced. Several factors do not favour the production of meal from capelin: the shortness of the

season when they are available, the low fat content, 3 to 4%, and the high water content of about 80% (Andrews, 1954). However, in recent years there has been a large increase in the amount of capelin used in the production of fish meal in Norway. Large schools of capelin can be detected by the echo-sounder well offshore, from the Newfoundland coast. If they can be seined at this time, it would extend the period of availability and favour the reduction industry.

DISTRIBUTION

Capelin are found in arctic and sub-arctic regions, but their distribution also extends into more southern localities. Figure 2 shows the world distribution of capelin. This map contains all the records of capelin captures that could be found from a fairly extensive survey of the literature. The most doubtful area is along the Northern Siberian Coast because it has been possible to consult only a small part of the Russian literature.

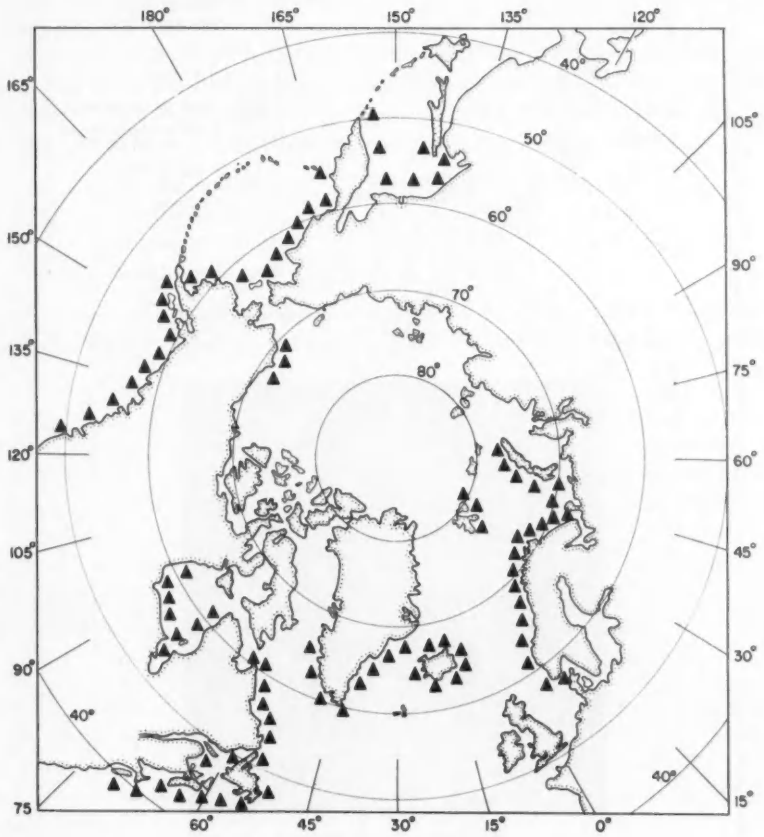

FIG. 2. World distribution of *Mallotus*.

In the area studied the distribution of capelin is as illustrated in Figure 3. Inshore, capelin are distributed along the coast of Newfoundland and Labrador to the north. Templeman (1948) reports capelin from as far north as Hebron and in 1950 the *Investigator II* took some at Nachvak.

Capelin are distributed over most bank areas. Most of the records of capelin capture were from the otter trawl with the cod end lined with 1¾-inch (44 mm.) stretched mesh shrimp netting. Commercial trawlers frequently take capelin in large quantities, particularly along the southern, the northern and northeastern parts of the bank. No capelin were taken on Flemish Cap, Banquereau or Sable

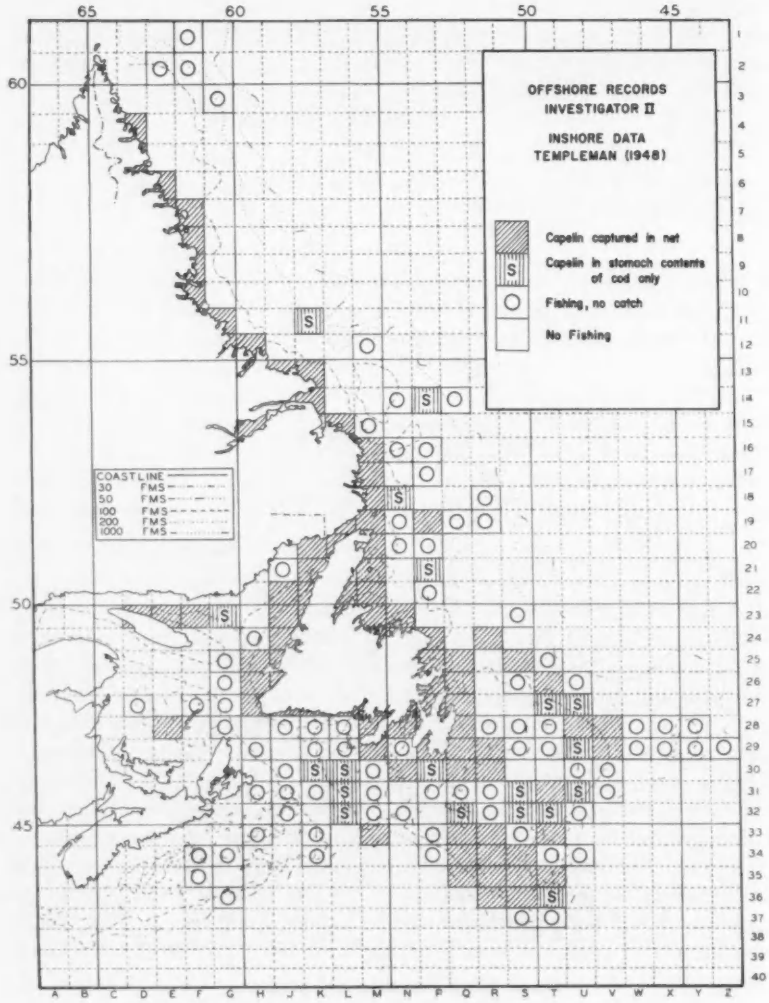
65
60
55
50
45
60
55
50
45
OFFSHORE RECORDS
INVESTIGATOR II
INSHORE DATA
TEMPLEMAN (1948)
Capelin captured in net
Capelin in stomach contents of cod only
Fishing, no catch
No Fishing
COASTLINE
30 FMS
50 FMS
100 FMS
200 FMS
1000 FMS
A B C D E F G H J K L M N P Q R S T U V W X Y Z
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40

FIG. 3. Distribution of *Mallotus villosus* in the Newfoundland area.

Island Bank either from the net or from the stomachs of cod. In general then, it can be stated that capelin are distributed over all the Grand and St. Pierre Banks as well as in the coastal region and in the deeper offshore waters.

SPAWNING

Bank Spawning

The first evidence of capelin spawning on the Grand Bank came from a sample of haddock taken by a commercial trawler on July 19, 1950, on the Southeast Shoal of the Grand Bank in the approximate position of lat. 44°25′N., long. 50°00′W. The stomachs and intestines of these specimens of haddock contained a large amount of sand mixed with capelin eggs. Also during this trip large numbers of mature capelin were caught. These were all partly spent or spent fish. Later in same year, August 5 to 10, and again on July 15, 1951, other samples of sand and spawn were secured from the same locality by the same method. Rass (1933) also secured capelin eggs from the stomachs of haddock in the Barents Sea.

The Southeast Shoal is the only bank area from which spawn was secured and it was from this locality that all the observations reported here were made. The temperature of the water on the bottom at an approximate depth of 25 to 27 fathoms (46 to 49 m.) where these samples were taken was as follows:

Southeast Shoal	July 19, 1950	2.8°C.
Southeast Shoal	Aug. 9, 1950	2.8°C.
Southeast Shoal	May 15, 1951	4.7°C.
Southeast Shoal	Aug. 10, 1951	4.2°C.

Figure 4 is a photograph of a sample of sand and spawn taken from a haddock stomach. Many of the eggs are still clinging to the sand. The grains of

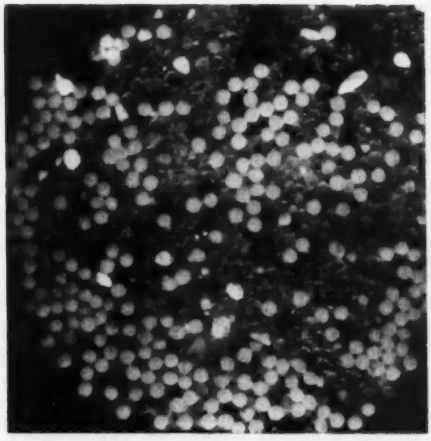

Fig. 4. Photograph of sand and capelin spawn taken from the stomach of a haddock from the Southeast Shoal of the Grand Bank, August, 1950.

sand were quartz-like in structure, quite smooth and ranged in diameter from 0.5 to 2.2 mm.

Comparison with Shore Spawning

The spawning of capelin close to the beaches around the coast of Newfoundland is a familiar sight during late June and the first two weeks of July. It has been described is some detail by Perley (1852), Jeffers (1931), Sleggs (1933) and Templeman (1948). Briefly, during the spawning act a male and female momentarily pair and rush towards the beach or sometimes one female is held between two males by the ledge-like spawning ridges of the latter. In all beach spawning there is a relationship with a wave rushing against the sand causing a water movement which seems to stimulate spawning. Jeffers (1931) states that the spawning of capelin increases when there is a surf and decreases when there is little or none. However, it is well known that, when water temperatures become too warm on the beach, spawning will continue in the deeper coastal waters. The details of the mating mechanism in offshore spawning are not known. There does not appear to be any rushing or crowding of large masses of fish against the sand or the bottom since no damage to the anal fin of bank capelin was noted, whereas inshore the stiff anal fins of the males are nearly always badly frayed.

For beach spawning Templeman (1948) states that the most favourable temperature ranged from 6.2 to 8.4°C. Templeman found that at Holyrood in Conception Bay on the east coast of Newfoundland, when the temperature fell to 5°C., very little spawning occurred. However, with a rise in temperature to 5.8 to 6.4°C. there was a marked increase in spawning activity. In June, 1953, at Topsail in Conception Bay, capelin were spawning in very large numbers with the water temperature 10°C. Sleggs (1933) says that "capelin rolled in the surf during the period of July 6–10, inclusive, when the temperature ranged between 8.6 and 10.7°C.". These observations are in marked contrast to the temperatures recorded during spawning on the Southeast Shoal where temperatures were as low as 2.8°C., and in neither of the two years for which we have records did the temperature rise as high as Templeman's minimum for beach spawning. It appears thus that capelin can adapt to a range of temperatures for their spawning activity and in this case are forced to spawn at the lower end of the temperature range.

That spawning does take place at the bottom on the bank is a reasonable assumption. Templeman (1948) shows that the inshore capelin lay their adhesive eggs on the bottom. The fact that sand and spawn as well as adult spawning capelin were secured from the stomachs of haddock caught in the region of the Southeast Shoal indicates that capelin also spawn on the bottom in bank areas. In samples of sand and spawn from the Grand Bank many eggs were still attached to the sand grains.

Not only is the depth at which spawning takes places different from that of beach spawning but the character of the bottom is also different. Sand from the bottom on which the bank capelin were spawning was 0.5 to 2.2 mm. in diameter. This is much smaller than that found most favourable for beach spawning where

the best spawning beaches are made up of gravel 5 to 15 mm. in diameter (Templeman, 1948). Capelin deposit their eggs inshore on rough gravel, whereas the sand from the bank is quite smooth. It seems possible that inshore some eggs are deposited on the finer sand, but by wave action, they are either buried below the coarser sand or washed out into deeper water. Capelin apparently have a preferred type of spawning bed, but their range of selectivity is perhaps wide.

Other Offshore Spawning Grounds

The above account of spawning refers to conditions on the Southeast Shoal of the Grand Bank. Reports from fishermen indicate a much larger concentration of capelin than usual in this location in 1950. This is not, however, the only spawning ground of capelin on the Grand Bank. Other specimens taken at various localities indicate that spawning on offshore banks is fairly widespread. On the eastern edge of the Grand Bank, lat. 45°38′N., long. 49°29′W., at 35 fathoms (64 m.), on July 21, 1949, 4 males and 25 females were taken. All the males were spent but with some residual milt in the *vas deferens*, while the females ranged from the condition in which a few eggs remained to that condition of one specimen in which the body cavity was nearly filled with eggs. On July 17, 1948, a group from the central area of the Grand Bank, lat. 45°48′N., long. 50°03′W., at 34 fathoms (62 m.), had both males and females in the ripe or partly spent condition, thus indicating that spawning was still in progress. On June 8, 1947, from St. Pierre Bank, lat. 45°24′N., long. 46°11′W., at 44 fathoms (80 m.), four males and one female were taken. These were definitely approaching maturity since the testes were full of tailed sperm and the eggs were approaching mature size. Also from St. Pierre Bank, lat. 46°18′N., long. 56°57′W., at 22 fathoms (40 m.), on July 2, 1949, ripe males and females were taken. Thus from all available evidence it would appear that capelin spawn at various places on the offshore bank areas provided that suitable bottom conditions are available at the proper depths. We have no records of spawning populations at very great depths.

LARVAL DEVELOPMENT

The collection of sand and spawn from the stomachs and intestines of haddock was reported in the preceding section. The eggs were collected from haddock caught on the Southeast Shoal of the Grand Bank in the approximate position of 44°25′N., 50°00′W. The dates of capture were July 19, 1950, August 5 to 10, 1950, and July 15, 1951. Since in all cases the eggs were from the stomachs and intestines of haddock, incubation of the eggs ceased immediately because of the action of the stomach juices. The stage of development reached by the embryos when examined was, because of this, the same as on the date of capture of the haddock.

A record of the results of the examination of these eggs is given in Figure 5. For purposes of comparison four "levels" or "stages" corresponding to the most distinctive points of development attained by the embryos were established. Samples of capelin eggs were collected from individual haddock and sub-samples

DATE :	NO LARVAL DEV. STAGE 0	STAGE 1	STAGE 2	STAGE 3	STAGE 4	TOTAL NO. SAMPLES
JULY 19 1950	6	0	0	0	0	6
AUG. 9–12 1950	40	11	2	1	0	54
JULY 15 1951	0	2	0	0	35	37

FIG. 5. Record of the maximum point of development of capelin eggs from samples taken in 1950 and 1951 on the Southeast Shoal of the Grand Bank. (In each sample 75 to 100 eggs were examined.)

of 75 to 100 eggs were examined. Figure 5 shows the number of samples with the maximum point of development as illustrated.

The first group, taken in July, 1950, showed no recognizable embryo development, but were apparently in early cleavage stages since just a small "cap" composed of a few cells could be distinguished in most eggs. The temperature of the water was 2.9°C. in the locality from which these eggs were taken. About 20 days later on August 9 to 12, 1950, the second group of egg samples was taken in the same depth and locality. Of the 54 samples taken 40 had no distinguishable larval stage, although other stages, probably late gastrula, could be seen. Eleven had the developing embryo as a small ridge extending part way around the yolk with, however, as yet no separation of head and tail. Two samples showed stages corresponding to Figure 6 (of the 1951 sample) with the head separate from the yolk. One sample had early eyed larvae and the embryo had made one complete turn about the yolk. The temperature at the point of capture was 2.8°C. The third group was taken one year later, on July 15, 1951. Of the 37 samples of eggs all but two had advanced eyed larval stages as shown in Figure 7. Here the eyes are quite well developed and the body shows typical larval pigmentation. Several of these dissected from the eggs, averaged 4.8 mm. in length. The remaining two samples were of stage 0 (Fig. 5). No temperature was taken at the exact date, but hydrographic data show that for August 10, 1951, the temperature in this locality was 4.2°C.

DEVELOPMENT IN RELATION TO TEMPERATURE

Temperatures were considerably lower over the Grand Bank in 1950 than in 1951. Although no comparative hydrographic sections for the southern bank areas are available, yet the sections across the Grand Bank at a more northerly

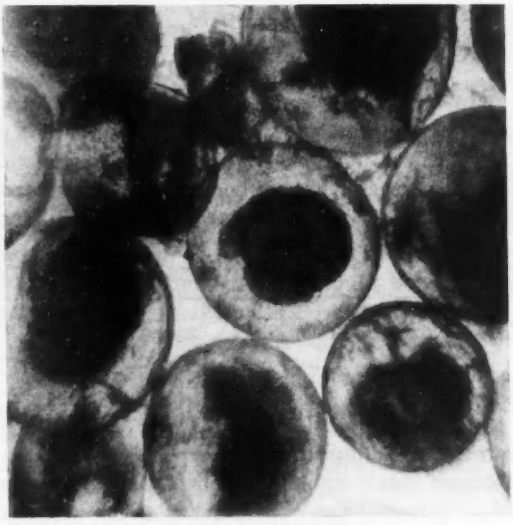

FIG. 6. Developing embryos of capelin collected on July 15, 1951.

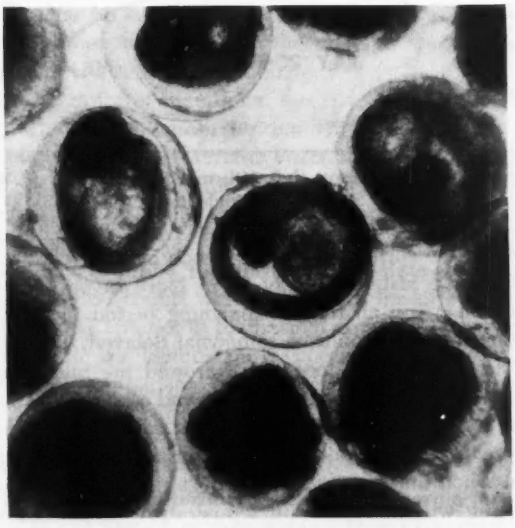

FIG. 7. Developing embryos of capelin collected on July 15, 1951.

locality (Fig. 8) indicate that a large mass of below –1°C. water covered most of this section of the bank in 1950, whereas in 1951 very little water colder than –1°C. was present.

It would be expected that cold water would delay the spawning act. However, bottom temperatures where spawning occurs during June and July may be as low at 2 or 3°C. yet at 15 fathoms (27 m.) the temperature may be 7 or 8°C., and 10°C. at the surface. Echo-soundings on various parts of the Grand Bank indicate the presence of schools of capelin up to 10 fathoms (18 m.) during

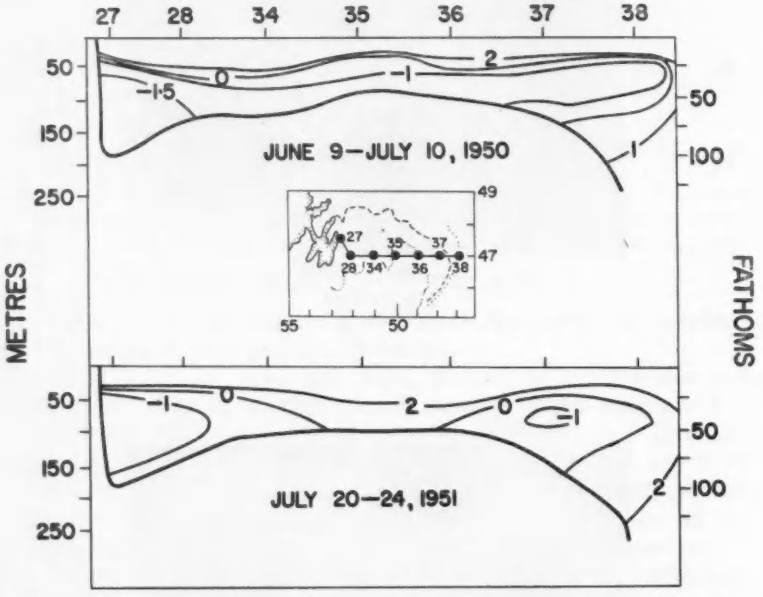

FIG. 8. Hydrographic section across the northern Grand Bank off St. John's and on the 47°N. latitude line.

the day and nearer the surface at night. Hence even in cold years the gonads could possibly develop just as quickly as in more favourable years. But it is unlikely that capelin spend all the pre-spawning period in the upper layer and thus in cold years spawning would be somewhat delayed. The 1950 spawning on the Southeast Shoal apparently took place around the middle of July whereas on the beaches spawning occurred in late June and early July. The 1951 spawning on the Southeast Shoal took place at about the same time as beach spawning. Possibly in cool years the fish wait as long as possible for a favourable spawning temperature, but when time passes and the eggs ripen the "pressure" becomes so great that spawning will take place in temperatures ordinarily unfavourable.

The second effect of low temperatures is to retard the development of the embryo and thus delay the time of hatching. In 1950 although spawning took

place at least around the middle of July, yet about one month later no embryos had reached stage 4 (Fig. 5). Jeffers (1931), from experiments carried out at Raleigh, Newfoundland, in 1927 and 1930, found that development was successful from 0° to 12°C. At 0°C. hatching occurred in about 55 days after fertilization; at 5°C. in about 30 days; at 10°C. in about 15 days, and at 12°C. in 9 days. At 2.9 and 2.8°C., the temperatures recorded in 1950 for the July 19 and August 9–12 samples respectively, development would proceed at a rate that would result in hatching in about 40 to 45 days after fertilization. This would put the time of hatching of the bulk of the eggs around the latter part of August or the first part of September. Hatching in 1951 would be expected to occur about the first of August judging from the size (4.8 mm.) of the dissected larvae. Templeman (1948) reports that recently hatched larvae measure about 3 to 6 mm. (from 5% formalin).

H. Dannevig (1895) showed that for cod and haddock the effect of a 1°C. change in temperature at 3 to 4°C. is nearly four times as great as a 1°C. change at temperatures 12°C. and above. The observation here from the field agrees with the above experimental work, since the water temperatures during the spring and summer of 1950 were on the average about 2°C. lower than in 1951 and the corresponding retardation of development in quite apparent.

VERTEBRAL COUNTS

Materials and Methods

The specimens used in this study were taken on various cruises of the research ship *Investigator II* and by certain commercial trawlers on which the Station had observers. All were taken in nets operated in connection with other researches or in commercial fishing. All the material was preserved in 5 to 10% formalin neutralized with sodium bicarbonate.

The method of capture, except for the specimens from stomachs, was by the otter trawl which has a mesh far too large to hold the capelin in large quantities, although in the last several years shrimp netting was used to line the cod-end. It is probable that the samples are unselected since the method of holding the fish was by being caught in various parts of the net and intermingled with other species.

In preparing and counting the vertebrae the flesh was removed from one side of the fish. Vertebral counts were made from the side from the first haemal arch to the hypural bone, anterior to the haemal arches the vertebrae were counted from below. Counts do not include the basioccipital nor the hypural bones.

For purposes of comparison the whole bank area has been divided into three sub-areas (Fig. 9).

Comparison between Bank Areas

Comparisons between the northern, central and southern parts of the Grand Bank are shown in the second part of Table I, but they involve different years in each area. Only one of the possible comparisons is formally "significant"—the 0.19 difference between northern and southern males ($P = 0.03$). However, no

FIG. 9. Average vertebral number for capelin from various localities. The inshore averages are from Templeman (1948).

certain significance can be attached to this because it is the extreme among several comparisons, and because the difference between the females in the same samples is in the other direction. Furthermore, the difference springs mostly from the presence of 1950 fish in the southern samples only, these having an exceptionally high count in both sexes.

Considering individual years, in 1947 the northern males had 0.24 more vertebrae than the southern ($P = 0.03$); but again the females showed the reverse pattern (the number of females was much smaller).

Comparison between Grand Bank and Inshore Areas

Vertebral averages for inshore areas are shown below (from Templeman 1948, see Fig. 9), together with the averages for all bank samples.

Area	*Vertebral average*	
	Male	Female
Labrador	65.53±.04	65.58±.04
East coast (N.)	65.45±.04	65.64±.04
East coast (S.)	65.56±.03	65.60±.04
S. and SW. coast	65.56±.03	65.72±.03
West Coast	65.43±.04	65.51±.04
Bank samples	65.48±.03	65.60±.05

The inshore counts were made on capelin taken in 1940 and 1941, and were for the most part of spawning fish.

For the males the inshore average which diverges most from the bank average is the east coast (S.) and the south and southwest coast. However, the differences are barely "significant", P being 0.05 in each case. For females, the inshore average for the south and southwest coast diverges most from the average for bank areas, but here again the difference (0.12 vertebrae) is only just "significant" ($P = 0.05$). Considering that these are comparisons of maximum differences, and that the year-classes compared are not the same, it is impossible to be sure that any consistent differences exist between bank capelin and those of any inshore area.

Comparison between Year-classes of the Same Area

Table I shows the vertebral averages of the year-classes making up the various samples. A comparison of year-classes should give some idea of the effects of the fluctuating environment on developing eggs. Unfortunately, with the available data is was possible to compare only a few groups.

For the southern Grand Bank the 1950 year-class males had 0.25 more vertebrae than did the combined samples of 1945, 1947 and 1958 with $P<0.01$; for females the difference was 0.31 in the same direction ($P = 0.04$). Between other year-classes of this area there are no significant differences nor are there any in the central or northern areas.

Discussion and Conclusions

It had been expected that the vertebral counts of capelin from the Grand Bank would be greatly different from those inshore since inshore eggs apparently develop in water temperatures that are 5 to 8°C. higher. However, such differences as have been shown are slight and of unproven significance. The 1950 year-class of the southern area is responsible for most of the differences found.

On the beach some embryos develop in water which may be in excess of 10°C., but it is quite possible that many are carried out into deeper and thus colder water before the critical period of segment establishment is reached. However, the average developmental temperature on or near the beach would still be considerably higher than on the bottom of the Grand Bank. The high counts for the 1950 year-class from the southern area apparently reflects the presence of cold water during that year as indicated in a previous section. No accurate records are available for the temperatures of other spawning grounds, but temperatures taken in the vicinity of the point of capture of spawning capelin in the central area of the Grand Bank on July 17, 1948 were 2.5 to 3.0°C.

TABLE I. Vertebral frequencies, averages, and standard errors of averages for capelin from the Grand Bank, arranged by year of hatch (year-classes).

		Male							Female							Male			Female		
Area	Year-class	62	63	64	65	66	67	68	62	63	64	65	66	67	68	Total	Average	Standard error	Total	Average	Standard error
Northern	1947	...	2	15	37	30	4	...	...	...	3	4	12	3	...	88	65.22	0.09	22	65.68	0.19
	1948	...	1	6	15	17	4	2	...	...	3	23	30	7	...	45	65.51	0.16	63	65.65	0.09
Central	1945	...	...	3	5	6	2	2	...	...	...	5	4	6	...	18	...	...	15	...	...
	1946	...	...	...	6	6	2	...	...	...	3	12	11	2	...	14	...	...	28	65.43	0.15
Southern	1945	...	1	2	8	8	1	...	1	1	1	6	3	1	2	20	65.30	0.21	15	...	...
	1947	1	4	54	154	164	41	5	...	2	8	15	22	7	...	423	65.46	0.05	54	65.44	0.14
	1948	...	...	6	26	26	5	1	...	...	3	14	10	4	...	64	65.52	0.11	31	65.48	0.15
	1950	...	...	7	42	40	20	2	...	...	4	17	30	8	1	111	65.71	0.09	60	65 75	0.11
Northern total		...	3	21	52	47	8	2	...	...	6	27	42	10	...	133	65.32	0.08	85	65.66	0.09
Central total		...	...	3	11	12	4	2	...	...	3	17	15	8	...	32	65.66	0.18	43	65.65	0.13
Southern total		1	5	69	230	238	67	8	1	3	16	52	65	20	3	618	65.51	0.04	160	65.56	0.08
Grand total		1	8	93	293	297	79	12	1	3	25	96	122	38	3	783	65.48	0.03	288	65.60	0.05

These temperatures are similar to those taken near known spawning areas of the Southeast Shoal in 1950. Although there are other records of spawning capelin being taken at various points on the bank, no records are available of the actual temperature conditions on the bottom where the eggs were developing, but it was without doubt much lower than on the beach. Because the vertebral averages of the 1950 year-class are significantly higher than those of other year-classes, it would appear that in many years, or at least in certain localities, eggs develop in warmer waters than those recorded on the Southeast Shoal in 1950.

The over-all picture, however, in spite of obvious temperature differences, does not point to consistently different vertebral counts between bank and shore capelin. This leads us to conclude that the whole mechanism of embryonic establishment of meristic parts is not entirely understood. Temperature, according to experiments by various workers, is a definite factor, but other factors, such as salinity, oxygen, hydrostatic pressure and carbon dioxide tension, may obscure the effects of the thermal conditions. Tåning (1952) showed that a decrease in both oxygen and carbon dioxide resulted in increases in vertebral number. The latter factor appears to have the greater effect on the number of segments produced. No information is available of the concentrations of these at the bottom on the Grand Bank or in inshore areas, thus it is not feasible to speculate further on the possible influence of these factors. The establishment of meristic parts is probably a complicated process especially for eggs developing on the bottom. On the other hand the cod vertebral numbers, with a pelagic egg, show an excellent correlation with temperature.

The fact that spawning definitely occurs in bank areas at the same time as beach spawning, indicates that one or more bank populations exist. Whether there is any mixing between bank and inshore populations is not known for certain, but it would appear likely that if any mixing does occur it would be between capelin of the northern bank area and those from the east and southeast coasts of Newfoundland. The pre-spawning period of shore capelin is apparently spent at some distance from the coast and in the deep water of the bays. Large numbers of capelin which were approaching the spawning stages were caught by the *Investigator II* in April and May along the northern edge of the Grand Bank. These could possibly be part of a shoreward movement, or they might have belonged to a population spawning in this locality–possibly near the Virgin Rocks.

Although the usual methods of race separation do not prove it, the general picture of capelin distribution seems to indicate a bank population, separate from those inshore, which on its more northerly fringes may have some mixing with inshore populations. Whether this bank population can be further broken down into discrete groups cannot at this time be stated.

Differences between Newfoundland Area Averages and Those from Widely Separate Areas

From a taxonomic point of view a comparison of the vertebral counts of *Mallotus* from widely separate areas of its circumpolar distribution is of some interest (Table II).

TABLE II. Comparison of vertebral averages of *Mallotus* from widely separated areas.

Area	Degrees N. latitude	Vertebral averages		Source
		Male	Female	
Newfoundland	43 to 55	65.43 to 65.67	65.51 to 65.72	This paper
British Columbia	48 to 55	65.32 to 65.76	65.05 to 65.24	Hart & McHugh (1944)
Greenland	60 to 70	68.07 to 68.32 (M & F)		Hansen (1943)
Iceland	65	69.48 (M & F)		Hansen (1943)
Murman Coast	67 to 72	70.83 to 71.54	69.72 to 71.12	Nikoforovsky (1933)

Pacific capelin have vertebral averages very similar to those of the Newfoundland area. The hypural half-segment was probably counted in the Murman and Greenland figures, but even if this is allowed for there would still be a very significant difference between them and the averages from the Newfoundland area.

It seems probable that the Murman capelin develop in temperatures just a little colder than the Grand Bank capelin, since Rass (1933) gave the spawning temperature as 2°C. in the Barents Sea, while the 1950 temperature near the spawning beds on the Southeast Shoal of the Grand Bank was about 2.8°C. However, this would not seem to account for the great differences in vertebral averages between these two localities. It may be that there are important environmental differences not yet recognized betwen the various areas, or else the capelin populations have considerable genetic differences. Experimentally only temperature has been shown to have such a profound influence, but as we have seen, there are other factors which may have an influence on the number of meristic parts that are produced.

SEX RATIOS

The separation of male and female capelin was by visual examination with the aid of a binocular microscope. In the immature fish the ovaries could be recognized with the naked eye by their lamellated structure. Recognition of testes was more difficult. In very immature fish they appear as very thin transparent strings lying close to the dorsal body wall. The testes sometimes were impossible to find before the fish were one year old unless sectioning was done, which would have destroyed the specimen for further study. Because of this the fish under one year which were caught previous to August were not used. When the eggs become developed enough to be distinguished, sex determination in the females was quite easy. At this stage also the testes are large enough to see and recognize readily.

In all but one pre-spawning sample there are more males than females (Table III). We doubt that net selection could cause this, since the greatest difference in size between male and female is in the two-year-old fish where the male exceeds the female by only 0.8 cm. Furthermore the changes in external body features resulting in larger anal and pectoral fins of the male, which would cause the latter to be more easily netted, are not yet present. It is possible that the very young fish have the sexes distributed selectively. However, the number

of fish examined was quite small and larger samples would perhaps give a different picture.

In *Mallotus villosus* during spawning and apparently for some time previous to this there appears to be considerable separation of the sexes with the result that highly disproportionate numbers of the sexes are found. Templeman (1948) found in a total of over 83,000 mature capelin that 71.8% were males. Samples taken when spawning was actually in progress were over 80% males, whereas those taken a short distance from the beach where no actual spawning was going on had sometimes as few as 20% males. A similar condition was found in

TABLE III. Number of male and female capelin in a variety of samples.

Area	Age	Date	No. male	No. female	Length M	Length F
	years				*cm.*	*cm.*
A. PRE-SPAWNING GROUPS						
West Grand Bank	2	Apr. 23/47	18	10	11.25	11.65
Southwest Grand Bank	2	Apr. 23/50	52	32	11.79	11.30
Central Grand Bank	2	July 17/48	12	5	10.63	...
Northeast Grand Bank	2	Aug. 5/49	86	20	15.30	14.50
North Grand Bank	1	Aug. 2/49	44	38	9.19	8.95
North Grand Bank	1	Sept. 8/49	28	22	9.34	9.48
Greenley Island	2	Sept. 16/51	10	10	12.25	12.10
South Grand Bank	2	Dec. 1/52	33	7	14.09	...
Total			283	144	...	...
B. SPAWNING GROUPS						
West Grand Bank	3	Mar. 29/51	15	3	16.33	...
North Edge Grand Bank	3	Apr. 15/51	57	83	15.37	14.67
South Grand Bank	3	Apr. 26/52	10	11	...	...
South Grand Bank	3	May 8/53	6	11	...	...
North Grand Bank	3	May 16/53	2	12	...	15.25
South Grand Bank	3	May 27/53	98	70	16.8	14.77
South-east Shoal	3	Aug. 5–10/50	423	54	17.70	15.20
Newfoundland inshore	3	Nov.–Dec., 1951 & 1952	10	237	...	...
Total			621	481	...	...

bank capelin that were spawning on the Southeast Shoal; 88.6% were males. In the latter case there may well have been a differential selection of one sex by the net because the female is smaller than the male and the male is thicker and has larger pectoral and anal fins.

The higher proportion of mature females in samples taken inshore in November and December after the spawning season may be because more males than females die as the result of injuries resulting from spawning on the beaches (Templeman, 1948). This refers, however, to inshore areas only, since very little experimental fishing was done on the Grand Bank during the autumn.

SUMMARY

1. Although capelin are used to a certain extent for human consumption and in the production of fish meal, yet their chief economic importance is as a food for other fish.

2. Capelin are found principally in arctic and sub-arctic regions, but their

distribution extends southward into more temperate regions. Distribution is general over most of the Grand Bank and St. Pierre Bank.

3. Capelin have a wide range of temperatures for successful spawning, from 2.8°C. on the Grand Bank to as high as 10°C. on the beach. On the beach spawning apparently ceases at 5°C.

4. The size of particles making up the bottom on which the bank capelin spawn ranged in size from 0.5 to 2.2 mm. and on the beach the size of the sand on the best spawning ground was 5 to 15 mm.

5. The effects of low temperature on spawning capelin are not only to delay the spawning period, but also to retard the development of the eggs and thus the time at which the larvae are released.

6. From the analysis of vertebral counts the following conclusions were reached: (a) It cannot be demonstrated that there is any significant difference between the vertebral averages of capelin from these different bank areas. (b) The Grand Bank averages are not significantly different from the inshore averages. (c) The differences that do exist between some year-classes are probably caused by differences in the temperature and other environmental conditions during egg or larval development.

7. The fact that capelin spawn some 200 miles from the coastal waters at the same time as the beach spawning is taking place, points to the presence of separate populations in bank areas.

8. In its world distribution *Mallotus* shows an increase in vertebral number from south to north which is not well correlated with developmental temperatures.

9. In non-spawning capelin samples, males were the more numerous. With the spawning capelin there appears to be a selective distribution of males and females.

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Age and Growth of the Capelin, *Mallotus villosus* (Müller), from Newfoundland and Grand Bank Areas[1,2]

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ABSTRACT

From the study of samples of capelin in their first year it was established that scales are acquired when the fish are a little less than one year old and range in size from 7.2 to 10.0 cm. total (extreme tip) length. Length frequency and age data indicate that there is great variation between the growth rates of the various year-classes.

From the Grand Bank 96% of the mature males and 99.6% of the mature females were three years old. No five-year-old fish were found on the Grand Bank. The average total lengths of mature capelin from bank and shore areas are quite similar.

The male capelin has a total length greater than that of the female. This difference increases from 0.22 cm. for one-year-old fish to 2.32 cm. for three-year-old spawning fish.

INTRODUCTION

Most of the previous work on capelin in the Newfoundland area by Jeffers (1931), Sleggs (1933), and Templeman (1948) was carried out on mature fish taken, for the most part, during a rather short period of the year. These authors confined most of their work to inshore samples since they had only limited access to samples from the deep water of the bays and coastal regions. In recent years during the cruises of the Biological Station's research vessel *Investigator II*, it was possible to collect capelin not only from the deep coastal waters, but also from various areas of the Grand Bank. Capelin of all age groups were taken and it is now possible to present some data on the growth rate and relative sizes of capelin from these groups. All the specimens used in this study were caught either in the otter trawl or were taken from the stomachs of other fish. Since 1950 the cod-end of the otter trawl has been lined with shrimp netting with a mesh size of 1¾ inches (44 mm.) stretched measure. However, the smaller capelin in particular were usually caught by entanglement with the rough, "hairy" manila twine of the trawl and were thus not meshed in the ordinary way. The shrimp netting will hold some of the larger capelin, but the holding capacity of the cod-end for capelin is influenced by the quantity of larger species present. Thus while we have no way of knowing if these samples are random, yet all sizes of capelin, from approximately 4½ cm. up to at least 20 cm., have been captured.

Age was determined from scales and otoliths when both were available. However, because most of the specimens were taken by the otter trawl with

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catches of larger fish, the rough treatment removed the scales from many fish. The easiest and most reliable method of age determination in capelin is by the use of otoliths because they are quite frequently more easily interpreted than scales. The localities where the specimens were captured are shown in Figure 1 and listed in Table I.

In recording the age of fish the method of "age-group" has been used. That is, a fish that was hatched in July belongs to the 0-group until the end of December. From January to December of the following year it belongs to the I-group and in succeeding years to the II-group, III-group, etc.

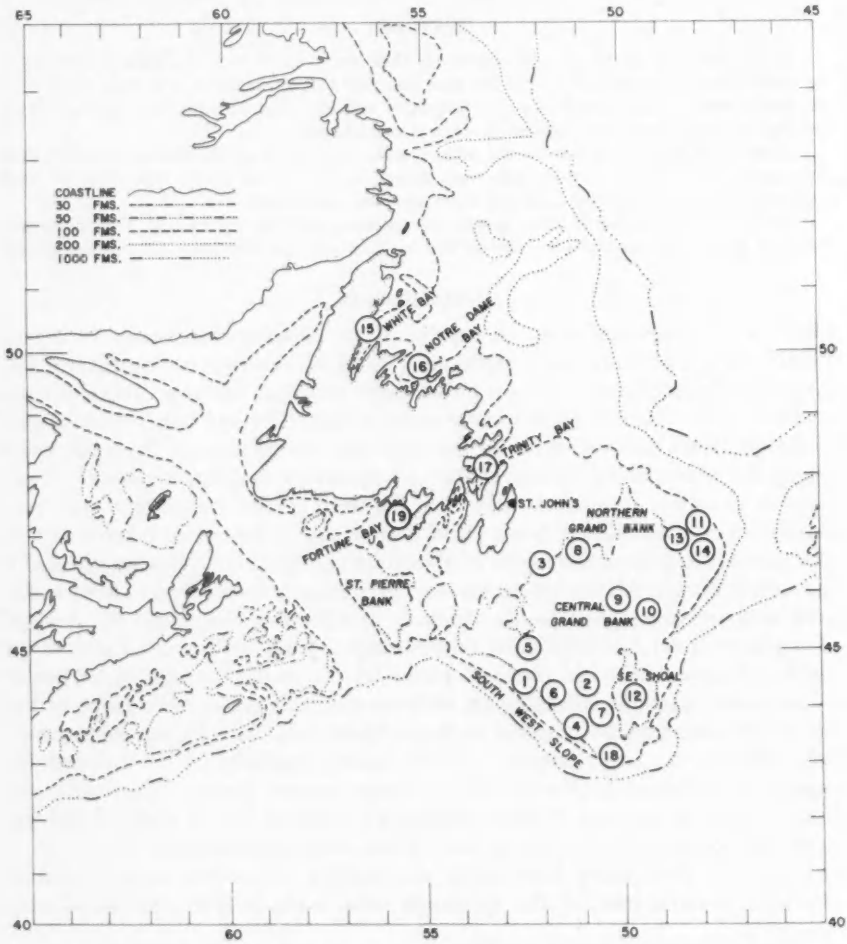


FIG. 1. Map of the Newfoundland area showing the localities from which samples were obtained. These are listed in Table II.

TABLE I. Origin of capelin samples used in this study. (OT = otter trawl; SC = stomach contents of larger fish.)

Sample number	Date	Depth	Position		Area	Number of capelin	How caught
			N. lat.	W. long.			
		fathoms				*no.*	
1	Mar. 29/51	45	44°22′	52°14′	W. Grand Bank	159	OT
2	Apr. 13/50	...	44°17′	51°04′	S. Central Grand Bank	136	OT
3	Apr. 14,15/51	56–64	46°28′	51°58′	N. Grand Bank	119	OT
4	Apr. 23/50	40	43°29′	51°07′	SW. Grand Bank	84	OT
5	Apr. 23/47	50	44°23′	52°20′	W. Grand Bank	28	OT
6	Apr. 26/52	46–45	44°09′	51°42′	SW. Grand Bank	19	OT
7	May 27/53	38–50	43°49′	53°10′	S. Grand Bank	168	OT
8	July 8/49	...	46°33′	51°19′	NW. Grand Bank	104	OT
9	July 17/48	32	45°48′	50°03′	Central Grand Bank	49	SC
10	July 21/49	34–35	45°38′	49°29′	Central Grand Bank	26	OT
11	Aug. 5/49	72	47°03′	48°11′	NE. Grand Bank	110	OT
12	Aug. 5–10/50	26	44°05′	50°00′	SE. Shoal	260	OT
13	Aug. 2/49	...	46°49′	48°34′	NE. Grand Bank	82	OT
14	Sept. 8/49	62	46°35′	48°03′	NE. Grand Bank	50	OT
15	Oct. 16/51	147–150	50°21′	56°19′	White Bay	51	OT
16	Nov. 14/51	180	Notre Dame Bay		...	18	SC, OT
17	Nov. 14/50	153	48°11′	52°05′	Trinity Bay	38	OT
18	Dec. 1/52	65–76	42°58′	50°20′	S. Grand Bank	40	SC
19	Nov. 24–30/52	100–180	47°12′	55°45′	Fortune Bay	143	OT

The lengths recorded are all total lengths. This was measured from the tip of the mandible which projects in front of the snout, to the long ventral lobe of the caudal fin with this lobe extended backward. Measurements were to the nearest millimetre. Sizes were then grouped into half-centimetre groups.

DETERMINATION OF AGE

TIME OF YEAR AND SIZE OF FISH AT THE APPEARANCE OF SCALES

Before scales can be used in age determination it is necessary to know when the scales are first developed. The approximate time of year and the size and age at which capelin acquire scales has been established by the study of four samples of I-group capelin. These are shown in summary in Table II. These groups were taken at different times of the year from various areas of the Grand Bank. The capelin were captured by otter trawl and were sometimes intermingled with other larger species. A variety of sizes from the adult down to about 4 cm. were captured in this way.

In examining small capelin for scales the following method was used. The surface of the fish was examined under a low-power binocular microscope and gently scraped with a fine scalpel. Any scales found were quite readily seen and the scale pockets were easily distinguishable after the gloss on the surface had been removed. These pockets appeared as overlapping blotches. No staining of the tissue was carried out, since it was necessary to examine a fairly large number of fish as rapidly as possible, and retain the specimens for further study.

Scales were first found on the posterior two-thirds of the fish near the lateral line. The first evidence of scales was found on fish of 7.2–10.0 cm., taken in July. Fish without scales in this sample measured 5.0–7.7 cm. After July all fish had scales.

The presence of scale pockets was considered to be a sufficient criterion that scales had formed. Thomson (1904), in his survey of the literature on scale formation, states that the formation of scale pockets takes place just after completion of the first layer of the scale when the embryonic scale changes it position and becomes embedded in the deep layer of the dermis. Paget (1920) also confirms that the formation of the scale pocket comes about early in scale formation. Huntsman (1918) reports that, in herring and alewife, scales first appear along the lateral line between the anal and caudal fins. Everhart (1949), working with smallmouth bass, found that scales appeared first just anterior to the anal fin along the lateral line. Neave (1936) and Elson (1939) found that, on two different species of trout, scales first appeared along most of the length of the lateral line. Scale formation in capelin is in agreement with most of the above work, the scales or scale pockets being first found in the posterior two-thirds of the fish in the region of the lateral line.

Since the sample on July 8 shows the presence of scales (Table II) it seems reasonable to put the time of scale appearance in capelin at around the latter part

TABLE II. Number of I-group capelin with scales (or scale pockets) present, and number in which they were absent. No fish of the March and April groups had scales (or pockets), and no fish of the August group lacked them.

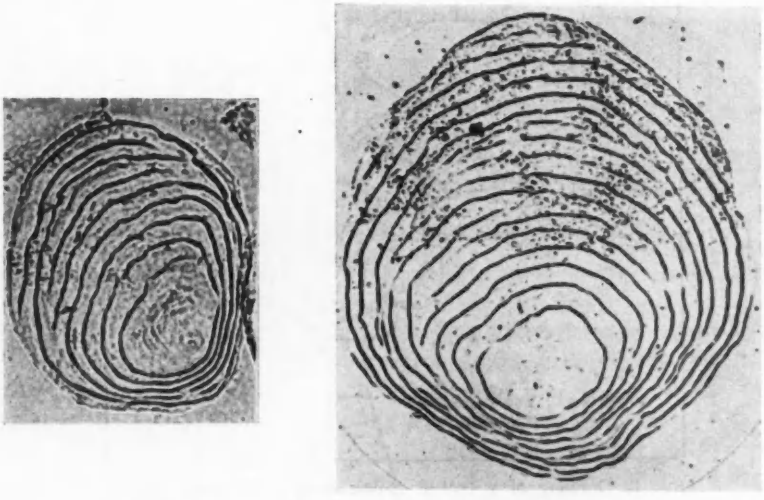
Length range	Western slope Grand Bank March 29, 1951	Southwest slope Grand Bank April 13, 1950	Northwest slope Grand Bank July 8, 1949		Northeast slope Grand Bank Aug. 2, 1949
	Absent	Absent	Absent	Present	Present
cm.					
4.3– 4.7	...	3	...	...	...
4.8– 5.2	...	41	1	...	...
5.3– 5.7	...	45	6	...	...
5.8– 6.2	5	22	5	...	...
6.3– 6.7	15	14	5	...	...
6.8– 7.2	57	10	7	1	...
7.3– 7.7	57	1	4	24	1
7.8– 8.2	5	...	...	22	7
8.3– 8.7	1	...	...	12	17
8.8– 9.2	1	...	...	6	25
9.3– 9.7	...	...	...	7	19
9.8–10.2	...	...	...	2	12
10.3–10.7	...	...	...	...	1
Total capelin	141	136	28	74	82
Av. size without scales, *cm.*	7.17	5.63	6.41	...	...
Av. size with scales, *cm.*	...	...	...	8.19	9.07

of June, at which time, judging from otolith readings, the fish would be from 10 to 12 months old. However, it would appear that both age and size are factors to be considered in the time of appearance of scales. In the 7½ to 9 cm. categories none of the fish had scales or scale pockets in March, whereas in July 94% had scales (Table II). In August all of these categories had scales thus indicating that the fish must be approximately one year old before scales are formed. On the other hand, although all the July sample had apparently reached the same age, no fish under 7.2 cm. had acquired scales. It is possible of course that fast-

growing fish, such as the March 29, 1951, sample (Table II) will put on scales earlier than slow-growing fish but no material was available to give any indication of this.

Interpretation of Annual Zones on Scales

Templeman (1948) found that the best scales for age determination were those above the posterior junction of the anal fin with the body and just below the lateral line. Scales from this location were used for age readings. Also the interpretation of annual zones was similar to that described by Templeman (1948), the "summer growth" being represented by several concentric circles or spirals and the retarded or winter growth by gradually decreasing crescentic lines. This type of scale is illustrated in Figure 2A. Sometimes scales were found with several winter lines extending around the central area where they may run together to form condensed regions which extend well around the anterior axis of the scale. The interpretation of new or "plus" growth at the scale edge usually is not easy in this type of scale, since the developing new growth ring may often be mistaken for "winter" lines (Fig. 2B). The growth of the scale usually begins at the posterior end and proceeds anteriorly, although in some scales new growth develops at the anterior end also and joins the posterior growth at the sides.



A B

Fig. 2. A. A scale from a 13.5 cm. fish captured in May, 1953. New or "plus" growth can be seen at the outer edge. This fish is in its second year (II-group) and was caught on the Northern Grand Bank. B. Scale with third winter growth complete, from an 18.1 cm. capelin captured during the spawning period at Alexis Bay, Labrador, July 20, 1941 (from Templeman, 1948). The true age of this fish was approximately 4 years (IV-group).

Interpretation of Annual Zones on Otoliths

Templeman (1948) describes the method of age determination using fresh otoliths (not preserved in formalin) in which the alternate opaque and translucent bands are quite distinct. As this author also points out, the otolith can, however, be read in another way. By holding the otolith at a slight angle a ridge corresponding to the opaque band and a groove corresponding to the translucent band can be seen, or in other words the ridge represents the rapid "summer" growth and the groove or hollow the slow "winter" growth. Figure 3 shows the shape of the typical capelin otolith. The central area of the otolith is not considered to be winter growth but merely the central nucleus of embryonic otolith development.

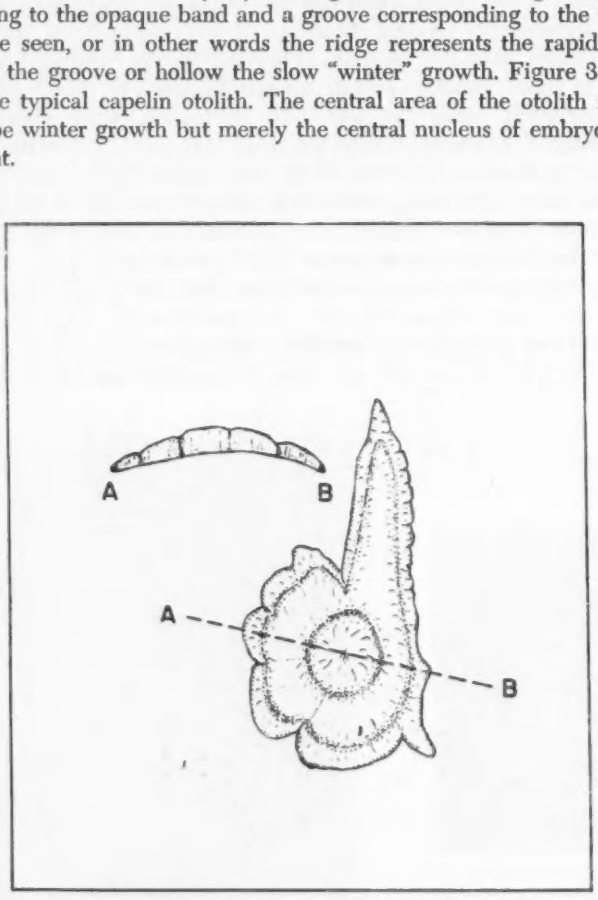


Fig. 3. Drawing of a typical otolith from a III-group capelin. Cross section illustrates the ridges and grooves corresponding to summer and winter growth respectively.

Nearly all the otoliths used in this study were from fish preserved in 5–10% formalin, hence the method of "ridges and grooves" as described above was used since the preservative renders the translucent bands opaque.

SIZES OF CAPELIN

The I-group

The lengths of capelin of the I-group at various months of the year are illustrated in Figure 4. Table III gives the length frequencies and average sizes of these. The fact that the average size of the March, 1951, sample was larger than that taken in April, 1950, and also nearly as large as the July, 1949, sample would seem to indicate that growth varies considerably between year-classes. Some of this difference in size attained by the March and April groups can apparently be attributed to the differences in water temperature during the

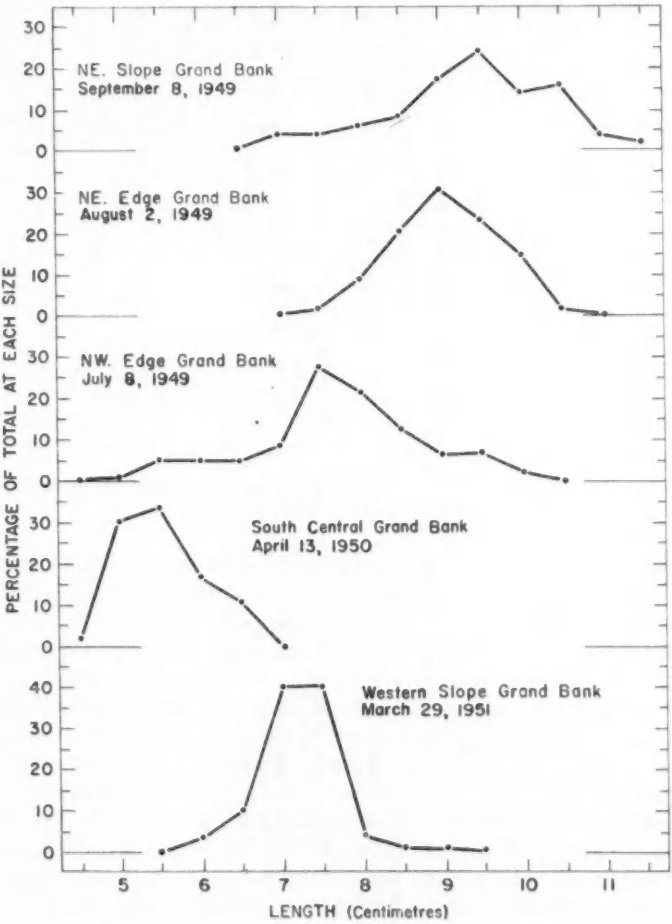


Fig. 4. Length frequencies of the I-group of capelin.

TABLE III. Length-frequencies of the I-group of capelin.

Number (Fig. 1)	Locality	Date of capture	Year-class	Number at each half-centimetre group															No. fish	Av. size
				4½	5	5½	6	6½	7	7½	8	8½	9	9½	10	10½	11	11½	12	
																				cm.
1	Western Grand Bank	Mar. 29, 1951	1950	...	...	...	5	15	57	57	5	1	1	...	...	...	...	...	...	141	7.17
2	S. Ctl. Grand Bank	Apr. 13, 1950	1949	3	41	45	22	14	10	1	...	...	...	...	...	...	...	...	...	136	5.64
8	NW. Grand Bank	July 8, 1949	1948	...	1	6	5	5	9	29	22	12	6	7	2	...	...	...	...	104	7.69
13	NE. Grand Bank	Aug. 2, 1949	1948	...	...	...	...	...	...	1	7	17	25	19	12	1	...	...	...	82	9.07
14	NE. Grand Bank	Sept. 8, 1949	1948	...	...	...	...	...	2	2	3	4	9	12	7	8	2	1	...	50	9.40

early spring of the year of capture. Spring hydrographic data for the Grand Bank for 1950 and 1951 are shown in Figure 5. In April, 1950, a large mass of water with temperatures 0°C. or less covered the greater part of the Grand Bank; and the Avalon Channel, between Newfoundland and the Grand Bank, was completely filled with water –1°C. and below. In contrast to this, on March 8 to 10, 1951, there was little –1°C. water in the Avalon Channel and the greater part of the water covering the Grand Bank had temperatures above 1°C. The actual bottom temperature taken at the time of capture of the April samples was 0.08°C. whereas that for the March sample was 2.40°C. These temperature differences,

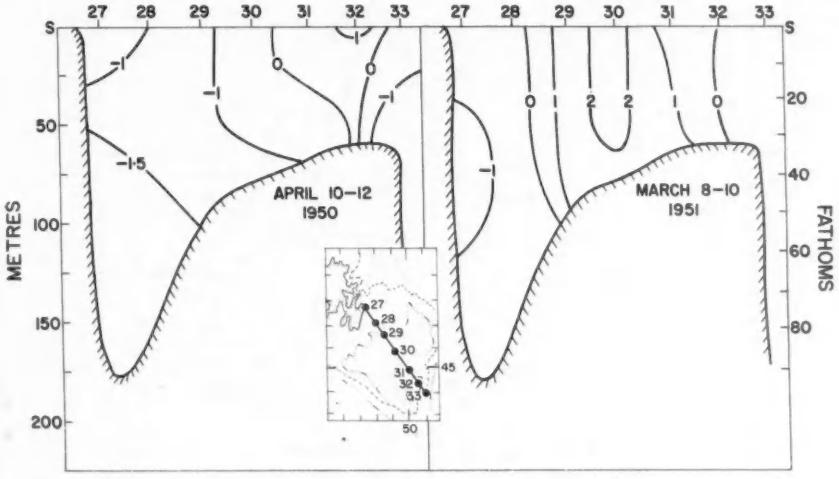


FIG. 5. Hydrographic section of the Grand Bank in the spring of 1950 and of 1951. Temperatures are in degrees Centigrade.

while accounting for some of the variation in size between the samples of two succeeding years, are probably not responsible for the complete growth picture. Growth during the autumn following the hatching period would probably vary considerably both between years and between localities. In the period following hatching the larvae are near the surface, and even in years when bottom and intermediate temperatures are lower than usual, as were the summer temperatures in 1950 (Pitt, 1958), the upper layers may have normal temperatures.

Between the July and August samples there appeared to have been more growth than in the period between the time of capture of the August and September groups. However, there is the possibility that the September sample may have reached a size where the larger fish are too large to be held by the rough manila twine and are too small to be retained, by the cod-end in any quantity. Another point which may contribute to the apparent change in growth rate is that, although these three samples belong to the same year-class, we are not sure that they belong to the same population. In Figure 1, the July sample

is No. 8, the August sample No. 13, and the September sample No. 14. No. 13 and 14 are close together and are likely to be from the same population but the July sample might well belong to a different one.

The II- and III-groups

The length frequencies of these age-groups are illustrated in Figures 6 and 7. Table IV lists the individual sample frequencies. These samples have been combined in monthly or 2-monthly categories and are listed in Table V. All the

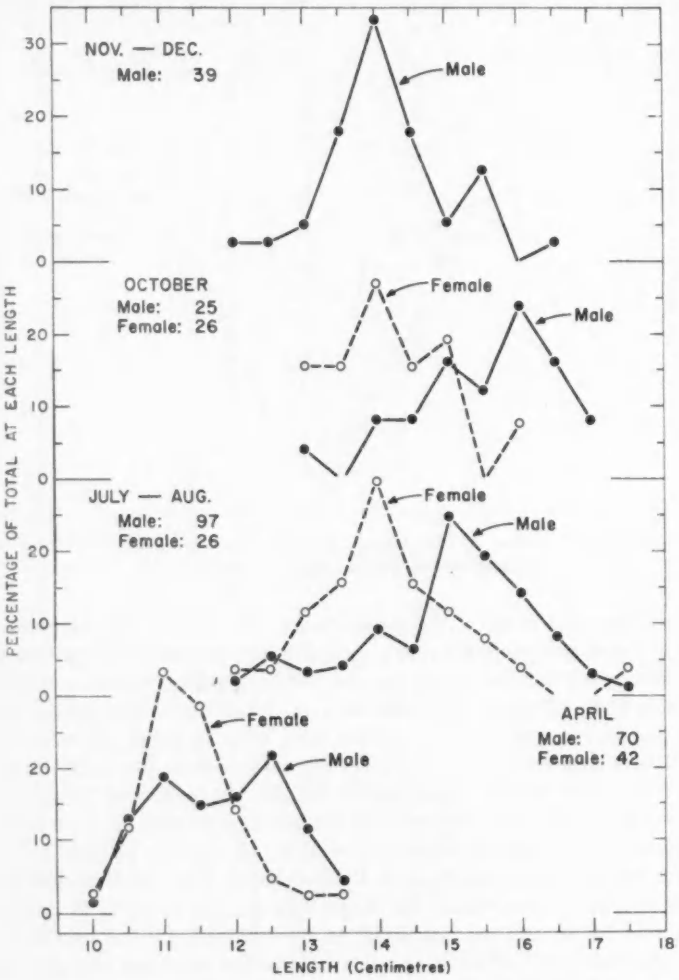


Fig. 6. Length frequencies of the II-group capelin combined in monthly or bi-monthly lots.

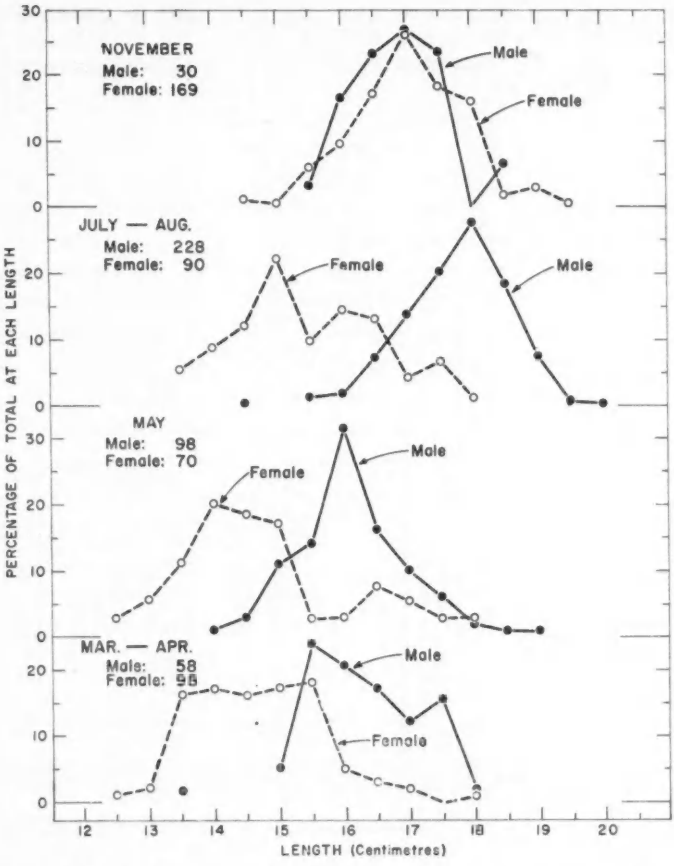


FIG. 7. Length frequencies of III-group capelin combined in monthly or bi-monthly lots.

II-group fish were sexually immature The III-group capelin, except for some immature males taken inshore in November and December, were all maturing, spawning or spent fish.

In both the II- and III-group the apparent rate of growth varies considerably. This variability could be due to several factors, particularly as the samples have been taken from different localities and were for the most part from different year-classes. The fact that the November–December III-group males are smaller than the July–August group can apparently be accounted for by the consideration that these males are immature fish which will spawn the following summer. These males do not necessarily constitute a whole slow-growing population, but rather a slower-growing and thus later-maturing segment of a population.

TABLE IV. Length-frequencies of individual samples of II- and III-group capelin from various localities.

Sample No. (Fig. 1)	Locality	Date of capture	Age-group	Year class	Number at each half-centimetre group: 10	10½	11	11½	12	12½	13	13½	14	14½	15	15½	16	16½	17	17½	18	18½	19	19½	20	Total fish	Av. length
																											No. cm.
												MALE															
1	W. Grand Bank	Mar. 29, 1951	III	1948											1	6	1		3	4						15	16.33
3	N. Grand Bank	Apr. 14 & 15, 1951	III	1948											2	7	10	7	4	5						35	16.27
4	SW. Grand Bank	Apr. 23, 1950	II	1948		7	11	7	9	10	6	2														52	11.79
5	W. Grand Bank	Apr. 23, 1947	II	1945	1	2	2	3	2	5	2	1														18	11.86
6	SW. Grand Bank	Apr. 26, 1952	III	1949								1				2	1	3			1					8	
7	S. Grand Bank	May 27, 1953	III	1950									1	3	11	14	31	16	10	6	2	1	1			96	16.13
9	Central Grand Bank	July 17, 1948	II	1946					2	5	3				2											12	
			III	1945															3	2	6	4	3			18	18.06
10	Eastern Grand Bank	July 21, 1949	III	1946																	1	1	1	1		4	
11	NE. Grand Bank	Aug. 5, 1949	II	1947									4	10	6	22	21	14	8	3	1					89	15.29
12	SE. Shoal	Aug. 5-10, 1950	III	1947											1		3	4	18	28	44	56	37	13	1	206	17.70
15	White Bay	Oct. 16, 1957	II	1949							1		2	2	4	3	6	4	2		1					25	15.62
16	Notre Dame Bay	Nov. 14, 1951	III	1948													2	2	3	2		1				10	
17	Trinity Bay	Nov. 22, 1953	II	1951									1	3			1		1							6	
			III														1	3	5	5	5		1			20	16.85
18	S. Grand Bank	Dec. 1, 1952	II	1950					1	1	2	6	10	7	2	4										33	14.09
												FEMALE															
1	N. Grand Bank	Mar. 29, 1951	III	1948											1	1	1									3	
3	N. Grand Bank	Apr. 14 & 15, 1951	III	1948						1	2	16	17	11	13	13	5	3	2		1					84	14.64
4	SW. Grand Bank	Apr. 23, 1950	II	1948	1	4	12	9	4	1		1														32	11.30
5	W. Grand Bank	Apr. 23, 1947	II	1945		1	2	3	2	1	1															10	
6	S. W. Grand Bank	Apr. 26, 1952	III	1949											4	3	4									11	
7	S. Grand Bank	May 27, 1953	III	1950						2	4	8	14	13	12	2	2	5	4	2	2					70	14.77
9	Central Grand Bank	July 17, 1948	II	1946					1	1	2		1													5	
			III	1945									1	1	2	2	2	3	1	2						14	16.93
10	Eastern Grand Bank	July 21, 1949	III	1946								1	2	5	4		3	2	2	2	1					22	15.55
11	NE. Grand Bank	Aug. 5, 1949	II	1947							1	4	5	4	3	2	1			1						21	14.50
12	SE. Shoal	Aug. 5–10, 1950	III	1947								4	5	6	14	7	8	7	1	2						54	15.28
15	White Bay	Oct. 16, 1951	II	1949							4	4	7	4	5		2									26	14.19
16	Notre Dame Bay	Nov. 14, 1951	III	1948										2	1	3		2								8	
17	Trinity Bay	Nov. 22, 1953	III	1950														2	6	2	7	1				18	17.47
18	S. Grand Bank	Dec. 2, 1952	II	1950					1		2	2				1	1									7	
19	Fortune Bay	Nov. 24–30, 1952	III	1949												7	16	25	38	29	20	2	5	1		143	17.08

TABLE VA. Length-frequencies of II-group capelin.

Month	Number at each half-centimetre group (total length)																Total	Average length
	10	10½	11	11½	12	12½	13	13½	14	14½	15	15½	16	16½	17	17½	18		
																		no.	*cm.*
									Males										
Apr.	1	9	13	10	11	15	18	3	...	...	...	...	...	...	...	...	...	80	11.96
July–Aug.	...	...	...	...	2	5	3	4	10	6	24	21	14	8	3	1	...	101	15.01
Oct.	...	...	...	...	...	...	1	...	2	2	4	3	6	4	2	...	1	25	15.62
Nov.–Dec.	...	...	...	...	1	1	2	7	13	7	2	5	...	1	...	...	...	39	14.17
									Females										
Apr.	1	5	14	12	6	2	1	1	...	...	...	...	...	...	...	...	...	42	11.38
July–Aug.	...	...	...	...	1	1	3	4	6	4	3	2	1	...	...	1	...	26	14.19
Oct.	...	...	...	...	...	...	4	4	7	4	5	...	2	...	...	...	...	26	14.19
Dec.	...	...	...	...	1	...	2	2	...	...	...	1	1	...	...	...	...	7	...

TABLE VB. Length-frequencies of III-group capelin.

Month	Number at each half-centimetre group (total length)																Total	Average length
	12	12½	13	13½	14	14½	15	15½	16	16½	17	17½	18	18½	19	19½	20		
																		no.	*cm.*
									MALE										
Mar.–Apr.	...	...	...	1	...	...	3	15	12	10	7	9	1	...	...	...	...	58	16.25
May	...	...	...	...	1	3	11	14	31	16	10	6	2	1	1	...	...	96	16.13
July–Aug.	...	...	...	...	...	1	...	3	4	18	31	46	63	42	17	2	1	228	17.75
Nov.	...	...	...	...	...	...	...	1	5	7	8	7	...	2	...	...	...	30	16.88
									FEMALE										
Mar.–Apr.	...	1	2	16	17	16	17	18	5	3	2	...	1	...	...	...	...	98	14.69
May	...	2	4	8	14	13	12	2	2	5	4	2	2	...	...	...	...	70	14.77
July–Aug.	...	...	...	5	8	12	20	9	13	12	4	6	1	...	...	...	...	90	15.44
Nov.	...	...	...	...	...	2	1	10	16	29	44	31	27	3	5	1	...	169	17.04

The IV- and V-Group Capelin

Templeman (1948) found that inshore, out of 1,557 spawning male capelin, 32.7% were from the IV-group and 0.3% were from the V-group, and of 952 spawning females, 27.8% were from the IV-group and 2.7% from the V-groups. The remainder were all of the II- and III-groups. These were all spawning fish. In comparison with this, of 400 mature or maturing males caught on the Grand Bank, only 16 or 4% were of the IV-group and there were none of the V-group; and out of 269 mature females only one (0.4%) IV-group fish was found. Examination of capelin caught in such areas as Trinity Bay and Fortune Bay during November and December, revealed that just about all the females belonged to the III-group and the condition of the ovaries indicated a previous spawning and also that they would spawn again the following spring. The III-group males, taken inshore in December, had not spawned. Inshore apparently more females survive the spawning act than in offshore areas. On the Grand Bank nearly all mature at three years since there is no evidence of males spawning more than once.

Comparison between Inshore and Grand Bank Growth

In making this comparison it has not been possible to compare fish of the same year-class. Furthermore the only period of the year for which inshore sizes are available is during the spawning period—June and July. There is little difference between the inshore and Grand Bank length frequencies for the II- and III-groups (Table VI).

Table VI. Average size of inshore and bank capelin. Inshore measurements are from Templeman (1948). (Numbers in parentheses are number of fish.)

Age-group	Total length, inshore, July, 1940 and 1941		Total length on Grand Bank, July–Aug., 1948–1950	
	Male	Female	Male	Female
	cm.	*cm.*	*cm.*	*cm.*
II	15.97 (17)	14.18 (40)	15.01 (101)	14.19 (26)
III	17.49 (1,020),	15.88 (621)	17.75 (228)	15.44 (90)

The Grand Bank II-group used in this comparison were all immature whereas the inshore II-group were mature.

Evidently the growth rates of capelin from inshore and bank areas differ very little. Temperature and food are usually considered to be the chief factors of the environment which affect growth rate, hence the inshore and bank capelin probably live in their brief lives under similar temperature and food conditions. Although inshore temperatures in the summer are higher than those in many bank areas, the inshore capelin are found close to shore for only the brief spawning period. Most growth takes place when the capelin is in the I- and II-age-groups when they apparently live in deep coastal waters where the temperatures are comparable to those of the Grand Bank.

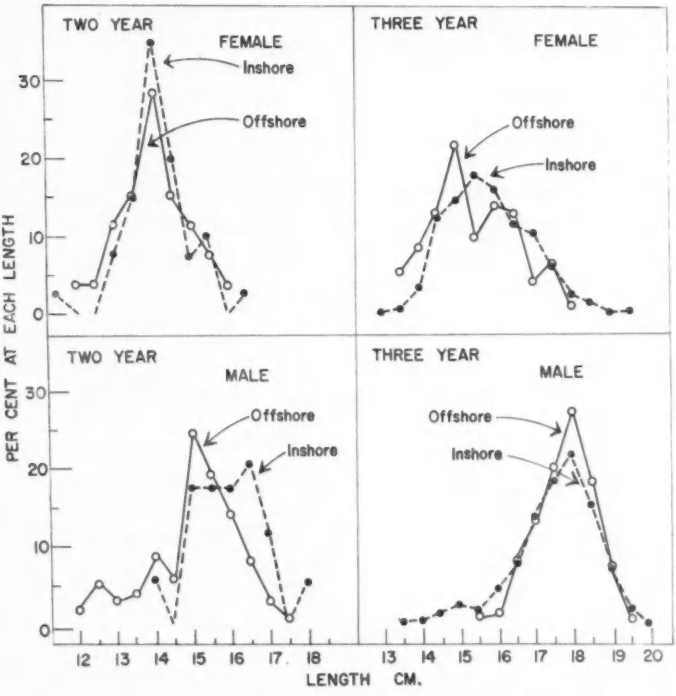


FIG. 8. Comparison of the sizes of II- and III-group capelin. The inshore fish were taken during the latter part of June and the first of July. The offshore fish were captured in July and August. (Inshore data from Templeman, 1948.)

DIFFERENCES BETWEEN THE LENGTHS OF MALE AND FEMALE CAPELIN

Table VII lists the average lengths of male and female capelin by 2-monthly periods. The I-group males and females differ very little, but afterwards the males grow faster than the females. This difference in size increases and reaches

TABLE VII. Comparison of the average total length of male and female capelin of the I-, II- and III-groups. (Standard errors and numbers of capelin are shown to the right of total length.)

Group	Age-group	Average length male		Average length female		Difference length of male length of female
		cm.		*cm.*		*cm.*
July–Aug.	I	9.17±.08	(44)	8.95±.13	(38)	0.22
Sept.–Oct.	I	9.34±.22	(28)	9.48±.22	(22)	−0.14
Mar.–Apr.	II	11.81±.11	(70)	11.38±.11	(42)	0.43
July–Aug.	II	15.01±.16	(101)	14.19±.23	(26)	0.72
Sept.–Oct.	II	16.62±.22	(25)	14.19±.18	(26)	1.43
Mar.–Apr.	III	16.25±.11	(58)	14.69±.10	(98)	1.56
May–June	III	16.18±.07	(98)	14.67±.13	(70)	1.52
July–Aug.	III	17.75±.05	(228)	15.44±.12	(90)	2.31

its maximum during the spawning period. Other differences between the sexes are the enlarged spawning ridges and anal fins of the male.

Discussions and Conclusions

Ages derived from scales and otoliths are in close agreement with the length frequency data. Hansen (1943) gives some excellent photographs of fresh otoliths from *Mallotus villosus* from West Greenland. However, his age interpretation differs somewhat from that recorded here. He appears to interpret the I-group as in this paper, if his photographs are on the same scale. The III-, IV- and V-group otoliths of his photographs would be interpreted here as II-, III- and IV-group capelin respectively. Apparently, Hansen reads as the first "winter" a tiny central translucent ring which is not considered here to be a "winter" but merely the central nucleus of otolith development. By the ridge and groove method of age interpretation, this central area of the otolith appears as a slight depression.

The general picture of capelin growth seems to be one of variation between year-classes which is probably related to the prevailing temperature and food conditions. The total period of growth is short—most taking place while the capelin are in the I- and II-age-groups, hence an adverse year will show more effect in capelin than in fish with a longer life span.

Acknowledgments

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The Fecundity Of Pacific Herring (*Clupea pallasi*) in British Columbia Coastal Waters[1]

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ABSTRACT

The fecundity of Pacific herring was investigated from a collection of 600 ovaries gathered from various localities along the British Columbia coast during the winter and early spring of 1954–55. It was found that fecundity depended mainly on body length and to a lesser extent on age, independently of its effect on body length. Certain differences in fecundity, found between herring from various localities when the relationship of fecundity to body length was considered, were not found when the relationship between fecundity, body length and age was considered. These differences were attributed to differences in growth rate. Fecundity of herring of same body length and the same age was found to be significantly higher in northern British Columbia than in southern.

INTRODUCTION

In late autumn and winter, Pacific herring (*Clupea pallasi*) move into inshore waters on their pre-spawning migration. Here they concentrate in large schools and are the object of an intensive fishery. Spawning occurs in late winter and early spring (mid-January to mid-April), shortly after the close of the fishing season. The adhesive spawn is deposited on vegetation in, or just below, the intertidal zone.

Each year since 1937 a survey has been made of the amount of herring spawn deposited along the entire British Columbia coast. The length and width of each spawning ground are measured and the intensity of deposition estimated. The results of the annual spawn surveys provide information on the initial size of the new year-class and form the basis for an index to the relative size of the spawning population, which, as spawning occurs shortly after the close of the fishery, is also an index to the size of the escapement from the fishery. While such an index is useful, an estimate of the size of the spawning stock in numbers of fish is more desirable. One method of estimating the size of the spawning stock is to translate the total numbers of eggs deposited into the number of fish responsible, using information on the mean number of eggs spawned per female, and the sex ratio. While information on sex ratio is readily available, the only information on egg production in British Columbia herring is for seven females examined by Hart and Tester (1934). There is also little information on the manner in which fecundity varies with body length and age, or from population to population. The purpose of the present study was to obtain additional information on the fecundity of British Columbia herring, on the relationship between fecundity and body length and age and on the variation, if any, in mean fecundity between populations. In the course of the study certain information was also

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obtained on the variation in size of mature herring eggs and on the relation between egg size and spawning time.

MATERIALS AND METHODS

Ovaries were collected from about 10 fish of each age-class from as many populations as possible. The collections were made during the regular annual sampling programme for age composition and growth studies. All samples were taken by purse-seine, except for the Walker Rock sample which was taken by otter trawl. As age determinations were not made until after the sampling process was completed, ovaries were obtained from females selected on the basis of length categories determined from age-length relationships. If the required number of females in each length category could not be obtained from a sample, additional fish were taken either from other samples from the same locality or from samples from another locality within the limits of the population. Because of the desirability of obtaining as mature fish as possible, the collection of ovaries was not begun until late December, 1954. This reduced the number of samples available in certain areas and in some cases made it impossible to obtain the desired number of ovaries. Ovaries were taken from a total of 600 herring, between December, 1954, and April, 1955.

For each sample, the statistical area, the locality, date of capture, and the number of ovaries obtained are given in Table I.[3] Figure 1 is a map of British Columbia, showing the sub-districts, statistical areas, and localities where samples were taken.

The samples from Departure Bay, Deep Bay, and Ladysmith were obtained from fish in the act of spawning. As these fish were undoubtedly partly spawned they could not be used in the fecundity study although, as will be discussed later, they provided useful information on the size-range of mature herring eggs. The samples from Cousins Inlet, Kildilt Sound, Klaskish Inlet, and Thompson Bay were discarded as they were too small to be representative. The sample from Meyers Pass was also not considered representative. Although this sample contained 22 fish, 20 of them were from a single age-class (Table III).

The body length of each fish, measured from the tip of the snout to the end of the silvery area on the caudal peduncle, was recorded to the nearest millimeter, and the weight to the nearest gram. The age was determined from scales.

From each fish, both ovaries were removed and preserved in Gilson's fluid to soften the ovarian tissue and facilitate the separation of the eggs. After a period of preservation, the ovaries were broken up manually, and by repeated washing and decanting, the majority of the ovarian tissue was removed and the eggs separated from each other. The remainder of the ovarian tissue was eliminated by washing the eggs through wire gauze. After filtering off the excess moisture, the eggs and filter paper were dried in an oven for 24 hours at a temperature of about 40°C.

The total number of eggs in a female was determined from the total weight of the ovaries and the mean weight of two 250-egg sub-samples. Weights were recorded to the nearest 0.0001 gram. When the sub-sample weight was less than

[3]Tables are at end of the paper.

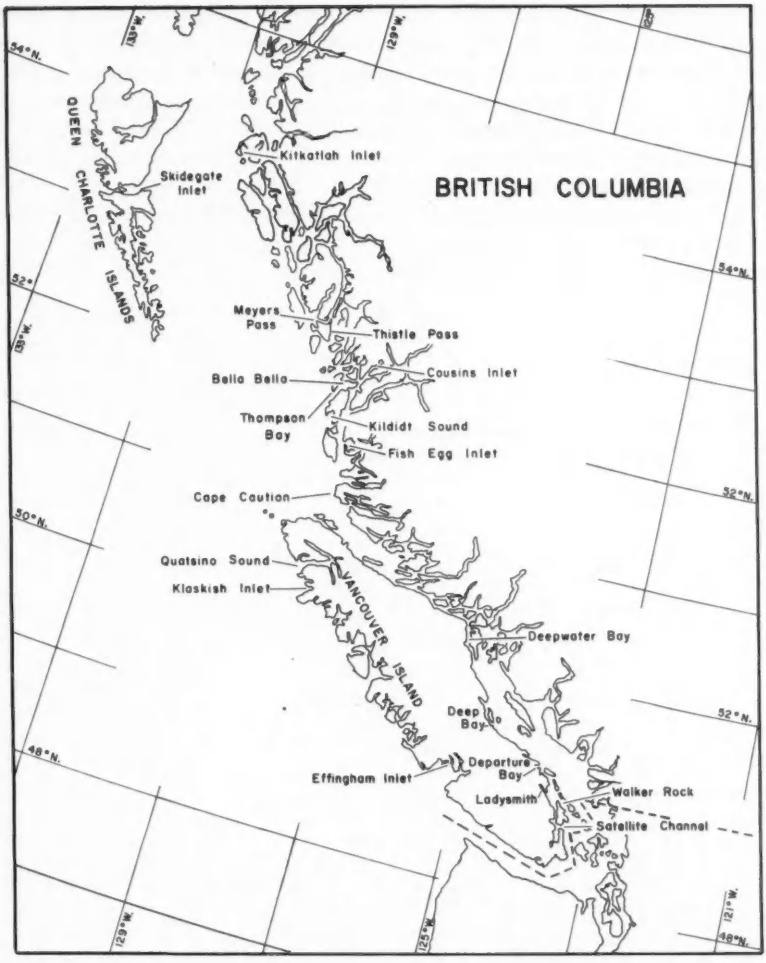

FIG. 1. Map of British Columbia, showing sub-districts, statistical areas, and localities where samples were taken.

0.0100 gram, the eggs were too small for the counts to be considered reliable. These immature ovaries were discarded. The variation in weight of 250-egg sub-samples from the same ovary was small. In 12 sub-samples taken from one pair of ovaries, the mean weight was 0.05355 gram with a standard deviation of $\pm$0.00095 gram; in 10 from another pair of ovaries, the mean weight was 0.02527 gram with a standard deviation of $\pm$0.00130 gram. In the first case the standard deviation was 1.8% of the mean, in the second 5.1%. The mean weight of two sub-samples is, therefore, a reasonably reliable estimate of the weight of 250 eggs.

MATURITY OF OVARIES

As herring eggs mature they increase in size and in weight. The weights of the 250-egg sub-samples, therefore, can be used as an index of the degree of maturity of the fish. These weights were grouped into nine categories of 0.0100 gram intervals from 0.0000–0.0099 gram to 0.0800–0.0899 gram. Table II shows, for each sample of fish, the number of ovaries assigned to each category. Of the 20 samples, 17 were taken from fish which had not yet spawned and 3 from fish in the act of spawning. In Figure 2, the number of eggs in each fish in the spawning samples, expressed as a percentage of the average number of eggs for a fish of the same length in the pre-spawning sample from the same sub-district,

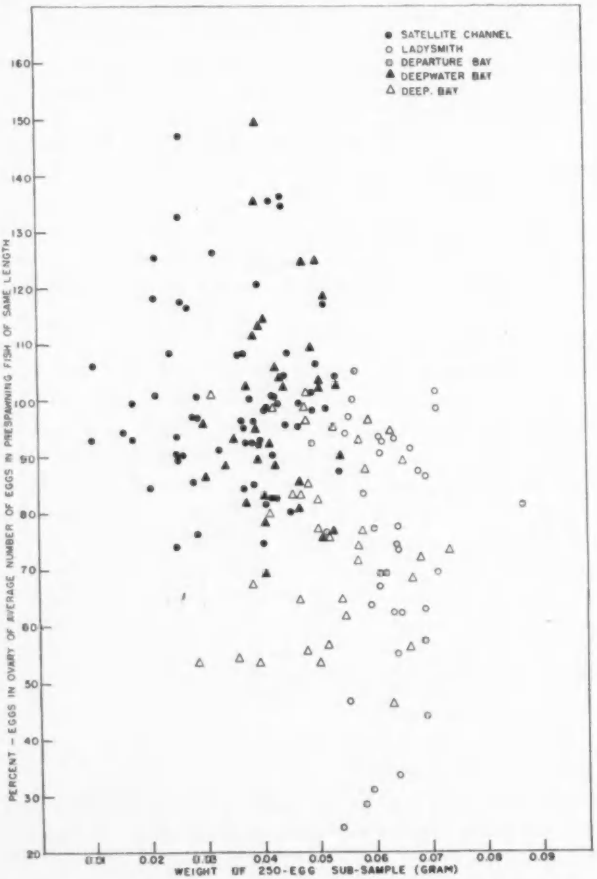

FIG. 2. The relationship between sub-sample weight and the number of eggs, expressed as a percent of the average number of eggs in a pre-spawning fish of the same length.

is plotted against the weight of the ovary sub-sample. For the Ladysmith and Departure Bay spawning samples, the Satellite Channel pre-spawning sample was used, and for the Deep Bay spawning sample, the Deepwater Bay pre-spawning sample was used. The average number of eggs in a fish of given length was determined from the curves in Figure 3. For comparison, the number of eggs in each fish in the two pre-spawning samples chosen was treated in the same way.

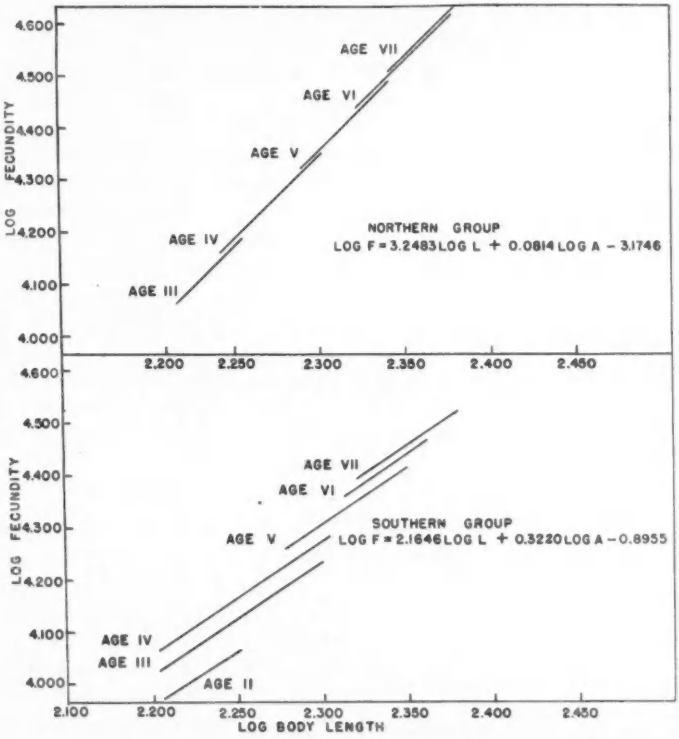

FIG. 3. The relationship of log fecundity with log body length and log age in the northern (top) and southern (bottom) groups of samples.

The great variation in the number of eggs in the fish of the same length is reflected in the wide range in percentages. In the pre-spawning samples, the percentages ranged from 70 to 150%, with the majority lying between 80 and 120%. In the spawning samples the percentages ranged from less than 20% to 100%, with the majority lying between 40 and 95%. The difference between the pre-spawning and spawning samples indicates that probably most or all fish in the spawning samples had partially spawned. The Ladysmith and Departure Bay fish on the whole contained less eggs than the Deep Bay fish. This possibly represents a difference in time between the start of spawning and the moment

when the sample was taken. In the 17 pre-spawning samples, the weights of the ovary sub-samples in Table II ranged down to less than 0.0100 gram and in only one individual exceeded 0.0600 gram. In the three samples from spawning fish, the weights of the ovary sub-samples ranged from 0.0200 gram to 0.0899 gram, indicating that there is a wide range in size of mature herring eggs. The overlap in the range in weights of the 250-egg sub-samples between pre-spawning and spawning samples suggests that the eggs may be mature for some time prior to spawning. Some factor other than the degree of maturity of eggs may also be required then to initiate spawning.

The data in Table II are not sufficient to determine whether or not there is a difference in the time at which herring in northern and southern British Columbia reach maturity. Outram (1955) has shown that, in general, spawning is later in the north than in the south. The herring in Effingham Inlet apparently mature earlier than those in the other localities sampled. Although this inlet is an important fishing ground, there have been no reports of herring spawning here in recent years. The herring apparently move out and spawn elsewhere in Barkley Sound.

The samples from Skidegate Inlet are interesting in that fish taken from December 6–14 were more mature than fish taken a month later between January 12–20. The marked difference in maturity suggests then that different bodies of fish were sampled and leads to the conclusion, either that two distinct bodies of fish were present in the inlet during the fishery or that the more mature fish moved out and were replaced by a less mature group.

RELATIONSHIP BETWEEN FECUNDITY, BODY LENGTH AND AGE

Table III shows the mean fecundity, the mean body length, and the ranges in fecundity and in body length by age-classes in each sample. Fecundity varies widely within an age-class and there is a considerable degree of overlapping in fecundity ranges between age-classes. Mean fecundity is greater in the older, larger fish. It is not apparent from this table whether the increased fecundity of older fish is the result of their greater age or their greater size. This question will now be examined.

Although a closer correlation probably exists between fecundity and body weight than between fecundity and body length (for example, in the Sattelite Channel sample the correlation coefficient between fecundity and body weight was + 0.8406 and between fecundity and body length was + 0.8027), body weight may vary with the state of maturity. Hart *et al.* (1940) showed that a considerable loss in weight occurred during the period when the eggs were being matured. Body length, on the other hand, is not affected by maturity, and as the samples were taken at various stages of maturity it is considered to be the more reliable criterion of size. As fecundity varies as a power of body length, and as a more directly proportional relationship was found between log body length and log age than between either log body length and age or body length and age, a logarithmic transformation was applied to all three variates to obtain straight-

line relationships and to equalize the variances throughout the ranges in body length and age. Logarithms to the base 10 were taken to 3 places in all cases.

Multiple regression (Snedecor, 1946) will permit the evaluation of the mutual relationship between fecundity, age, and body length. The relationship between them is expressed by the formula:

$$\log F = \log C + b_{y1.2} \log X_1 + b_{y2.1} \log X_2$$

where F = fecundity, X_1 = body length and X_2 = age, $b_{y1.2}$ = the coefficient of regression of log fecundity on log body length independently of log age, $b_{y2.1}$ = the coefficient of regression of log fecundity on log age independently of log body length.

Analysis of co-variance (Snedecor, 1946) was used to test the significance of differences between samples in the mean number of eggs adjusted to a common body length and common age. In the various comparisons, the significances of differences among sample mean fecundities adjusted to a common body length and a common age were tested. In each comparison, the appropriate mean square was obtained by dividing by the corresponding degrees of freedom the sum of squares of errors of estimate obtained by subtracting from the total sum of squares of errors of estimate the sum of squares of errors of estimate from the average regression within samples. This latter sum of squares was derived from the pooled sums of squares and products within samples. Each test was effected by using F to determine whether the mean square derived as above was significantly greater than that resulting by dividing the sum of squares of errors of estimate from the average regression within samples by its degrees of freedom. Table IV shows for each test the value of R^2, the degrees of freedom, the appropriate sums of squares of errors of estimate, the mean squares, and the value of F obtained.

No significant differences were found among the six samples from northern British Columbia (Skidegate Inlet, Kitkatlah Inlet, Thistle Pass, Bella Bella, Fish Egg Inlet, and Quatsino Sound), or among the the samples from southern British Columbia (Deepwater Bay, Satellite Channel, Walker Rock, and Effingham Inlet). Differences significant at levels less than the 0.01 level of probability were found between the combined northern British Columbia samples and the samples from Deepwater Bay, Satellite Channel, Walker Rock, and Effingham Inlet both separately and when combined to form the southern British Columbia sample. Fecundity in fish of the same body length and age was higher in the north than in the south.

The multiple regression equations for the northern and southern groups are:

$$\text{Northern: } F = 3.2483X_1 + 0.0814X_2 - 3.1746$$
$$\text{Southern: } F = 2.1646X_1 + 0.3220X_2 - 0.8955$$

where F = log fecundity, X_1 = log body length, and X_2 = log age.

In the following tabulation are shown, with their standard errors, the standard partial regression coefficients of log fecundity on log body length,

independent of log age, and of log fecundity on log age, independent of log body length for the northern and southern groups of samples.

	Standard partial regression coefficient	*Standard error*
Log fecundity on log body length		
Northern group	+ 0.7775	± 0.0579
Southern group	+ 0.5629	± 0.0775
Log fecundity on log age		
Northern group	+ 0.0488	± 0.0579
Southern group	+ 0.2789	± 0.0775

In both the northern and southern groups, the standard partial regression coefficient of log fecundity on log body length, independent of log age, differs significantly from zero ($t = 13.44$ & 7.24 respectively, $P<0.01$). In the northern group the standard partial regression coefficient of log fecundity on log age, independent of log body length does not differ significantly from zero whereas in the southern group it does ($t = 3.61$, $P<0.01$). Figure 3 shows the relationship of log fecundity with log body length and log age in both the combined northern British Columbia and combined southern British Columbia samples. Table V shows the average number of eggs in females of various lengths in each age-group in northern and southern British Columbia, calculated from the data in Figure I. Fecundity in fish of the same body length and age was higher in the north than in the south. It would also appear that whereas in the northern group there is no appreciable effect of age on fecundity, independent of its relation to body length, in southern British Columbia herring fecundity increases somewhat with age (considering fish of the same length). No obvious explanation has been found to account for this difference in the effect of age in the two groups. From a consideration of size of the regression coefficients and the relative size of the variates (of age and body length), it will be seen, however, that the effect of age alone on fecundity is very small even in southern British Columbia herring, and that for practical purposes, fecundity can be said to depend only on body length.

As the effect of age on fecundity, independently of its effect on body length, has been shown to be small, it is instructive to examine the relationship between fecundity and body length only. This relationship has been investigated in a number of species of fish, including the Atlantic herring (Hickling, 1940; Farran, 1938) and the Pacific herring from Puget Sound (Katz, 1947).

For the reasons given previously, a double logarithmic transformation was used. The relationship between log fecundity and log body length is expressed by the equation:

$$\log F = \log C + b \log L$$

Table VI shows for each sample the number of fish, the values of log C and of b, the regression coefficient or rate of change of log fecundity with log body length.

Analysis of covariance was used to test the significance of between-sample differences in intercept (log fecundity adjusted to a common log body length),

and in slope (rate of increase of log fecundity with log body length). For each combination of samples, tests were applied to determine whether the individual sample mean log fecundity deviated significantly from the line representing the average of the individual sample regressions (that is, whether there were significant differences in sample mean log fecundities adjusted to a common log body length) and whether there were significant differences among individual sample regression coefficients. In testing the significance of the adjusted sample mean log fecundities, F was used to determine whether the mean square derived from the sum of the squares of errors of estimate remaining when the sum of the squares of the errors of estimate calculated from the pooled sums of squares and products was subtracted from the total sum of squares of errors of estimate was significantly greater than the mean square associated with the average of the individual sample regressions. For testing differences in slope, F was used to determine whether the mean square for differences among individual sample regressions was significantly greater than the mean square for deviations from the average of sample regressions. Table VII shows for each test carried out the various sums of squares of errors of estimate, mean squares, appropriate degrees of freedom and values of F obtained.

No significant differences were found between the six samples from northern British Columbia (Skidegate Inlet, Kitkatlah Inlet, Thistle Pass, Bella Bella, Fish Egg Inlet, and Quatsino Sound). These samples were again grouped to form one large sample for northern British Columbia. Statistically significant differences were found between the four samples from southern British Columbia (Deepwater Bay, Satellite Channel, Walker Rock, and Effingham Inlet) and between each of these samples and the combined sample for northern British Columbia.

The results of these tests indicate that among herring from the Queen Charlotte Islands and northern British Columbia, as far south as the northern tip of Vancouver Island, there are no statistically significant differences in the relationship between fecundity and body length. There are, however, statistically significant differences between herring from northern and southern British Columbia, between herring from the upper and lower parts of the west coast of Vancouver Island, between herring from the central and southern parts of the east coast of Vancouver Island, and in the southern part of Vancouver Island between herring from the east and west coast. The results indicate that the fecundity of herring of the same body length decreases from north to south and in the southern part of the province from west to east. Figure 4 shows the relationship between fecundity and body length for herring from northern British Columbia, the central and southern east coast of Vancouver Island and the lower west coast of Vancouver Island.

The fact that statistically significant differences in fecundity exist between the four samples from southern British Columbia when the relationship with body length only is considered, but not when effects of body length and age together are considered, suggests that these differences are probably due to differences in growth pattern.

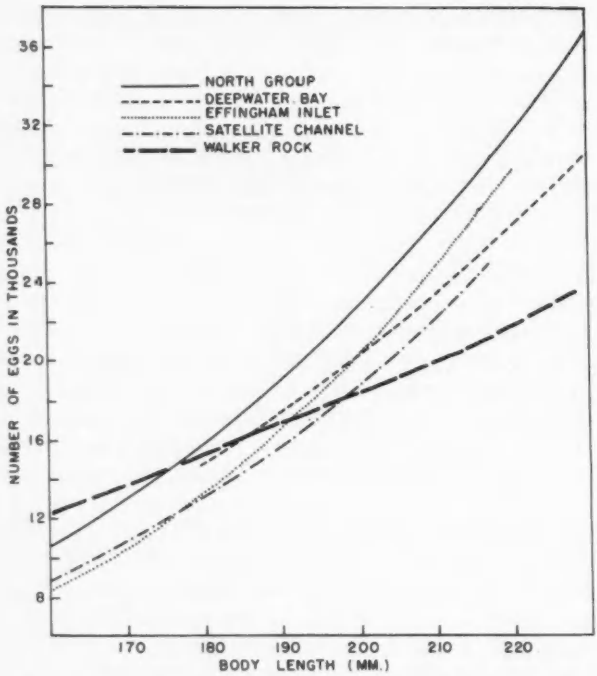

FIG. 4. The relationship between fecundity and body length in the northern group of samples and in the individual samples from southern British Columbia.

DISCUSSION

Fecundity in British Columbia herring, within populations, was found to vary mainly with body length and to a relatively minor extent with age independently of its effect on body length. Although the effect of age was very small, it was somewhat greater in southern British Columbia herring than in northern. The dependence of fecundity on the size of the fish and only to a minor degree on the age conforms with the results obtained in previous studies on the relationship between fecundity, body length, and age in other species of fish. Simpson (1951) found that in plaice, fecundity depended mainly on body length and that age alone, apart from its relation to size, appeared to have played an insignificant part. Raitt (1933) reported a somewhat similar situation in haddock, where fecundity depended mainly on the size of the fish but, in fish of the same size, was greater in the older fish. He found that the increase in reproductive capacity with age gradually declined and ceased when that age was reached at which all specimens of an age-class were spawners. Thereafter, there was some evidence of a slight decline in egg production. In the present samples, the older age-groups of herring were not sufficiently well represented to determine whether or not a similar decline in fecundity occurs with age among British Columbia herring.

It has been pointed out by Raitt (1933), Katz (1947), Simpson (1951) and others that the relationship between fecundity and body length is best expressed by an equation of the type: $F = CL^n$, and that the value of n is greater than 3. Ratt found in haddock that the best value for n lay between 3.2 and 3.3. Simpson assumed a value of 3 in plaice. Farron (1938), for Irish Sea herring, obtained a value of 4.5 and Hickling (1940), for southern North Sea herring, a value of 3.465. Katz, in Pacific herring from Puget Sound, found a value of n of 4.71. The values obtained in the present study lay generally between 3 and 4 (Table VI), differing somewhat from sample to sample. These values are considerably smaller than those obtained by Farron or Katz but correspond reasonably well with that obtained by Hickling.

Fecundity in fish of the same species has been found to vary from place to place. Simpson (1951) found that in North Sea plaice of the same body length, the faster growing fish from Flamborough area had a higher fecundity than the slower growing fish from the southern Bight. However, he believed that it was necessary to look in directions other than age or food for an explanation of the very high fecundity of Baltic Sea plaice. He considered that high fecundity was probably a characteristic of the Baltic race of plaice. This race was described by Poulsen (1932, 1939) and Blegvad (1935). Katz (1947) noted that Pacific herring from Seal Rock, Puget Sound, produced more eggs than British Columbia herring of the same length, and that the Siberian herring from Peter the Great Bay were less prolific egg producers than British Columbia herring of the same size. Considering fish of the same age, but not necessarily of the same size, Katz found that the fast-growing Siberian herring were far more fecund than either Puget Sound or Hokkaido herring. In general, the Japanese herring were more fecund than the Puget Sound fish of the same age up to 6 years, but after that age fecundities were more comparable. He considered that, regardless of differences in size, there were pronounced differences in fecundity of herring of the same age. He suggested that such differences might be a criterion for separating races. Farran (1938) and Hickling (1940) have shown that in fish of the same size there are significant differences in the number of eggs produced by the summer and winter spawning runs of European herring.

In the present study, when no consideration was given to the effect of age, it was found that fecundity in British Columbia herring of the same body length decreased from north to south and in the southern part of the province from west to east. However, when the independent effects of body length and age on fecundity were segregated, statistically significant differences in fecundity were found between herring from northern and southern British Columbia but not between herring from the middle and lower east coast of Vancouver Island. This suggests that the differences in the relation of fecundity and body length that existed between herring from these southern regions were due to differences in growth rate and that the differences between northern and southern British Columbia herring, while no doubt accentuated by differences in growth rate, were due to some factor other than body length and age.

Tester (1937), from a study of meristic characters, and Stevenson (1955), from an analysis of tag returns, both concluded that the British Columbia herring

stock consisted of a series of intergrading populations. The differences found in fecundity rather than indicating the presence of discrete populations, followed a pattern to be expected from a series of intergrading populations. Thus, when the effects of body length and age on fecundity were segregated, no significant differences in fecundity were found between populations relatively close together such as those to the north or to the south of Cape Caution, while statistically significant differences were found in mean fecundity in fish of the same age and body length between the populations at the extreme ends of the series, that is between the population-groups in northern and southern British Columbia.

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TABLE I. Number of ovaries sampled from each locality with date of capture and statistical area. Samples marked with an asterisk (*) were from spawning fish.

Sub-district	Statistical area	Locality	Date	Number of ovaries	Immature ovaries discarded
Queen Charlotte Islands	2A–E	Skidegate Inlet	Dec. 6, Jan. 12, 20	67	37
Northern	5	Kitkatlah Inlet	Jan. 21, 22, 30	62	3
Upper Central	6	Meyers Pass	Dec. 15	22	0
	6	Thistle Pass	Dec. 16	28	0
Lower Central	7	Thompson Bay	Jan. 6, 7	7	0
	7	Bella Bella	Jan. 9	37	3
	7	Kildidt Sound	Feb. 9	7	0
	8	Fish Egg Inlet	Dec. 16, 17	75	5
	8	Cousins Inlet	Jan. 13	10	6
Middle East Coast	13	Deepwater Bay	Jan. 18, Feb. 2	39	3
	14	Deep Bay*	Mar. 1, 9	37	1
Lower East Coast	17A	Departure Bay*	Apr. 5	10	0
	17B	Ladysmith*	Mar. 20	28	0
	17B	Walker Rock	Jan. 6, 20	29	0
	18	Satellite Channel	Jan. 5, 21, 24	71	0
Lower West Coast	23	Effingham Inlet	Jan. 12	26	0
Upper West Coast	27	Klaskish Inlet	Dec. 6	10	4
	27	Quatsino Sound	Dec. 6	35	0

TABLE II. Frequency distributions of weights of ovary sub-samples from herring taken in different localities. Samples marked with an asterisk (*) were from spawning fish.

Locality and date of sampling	Ovary sub-sample weight category (*milligrams*)										
	0 to 9.9	10.0 to 19.9	20.0 to 29.9	30.0 to 39.9	40.0 to 49.9	50.0 to 59.9	60.0 to 69.9	70.0 to 79.9	80.0 to 89.9	?	Total
Satellite Channel											
Jan. 5	...	2	9	4	5	...	...	...	...	...	20
Jan. 21, 24	2	2	10	13	18	6	...	...	...	...	51
Walker Rock											
Jan. 6	1	2	2	2	1	...	...	...	...	...	8
Jan. 20	...	4	3	4	8	1	...	...	...	...	20
Ladysmith*											
Mar. 20	...	...	...	...	1	7	16	3	1	...	28
Departure Bay*											
Apr. 5	...	...	...	...	...	5	5	...	...	...	10
Fish Egg Inlet											
Dec. 16, 17	9	37	27	2	...	...	...	...	...	...	75
Deepwater Bay											
Jan. 18–26	...	...	...	6	6	4	...	...	...	1	17
Feb. 2	...	1	1	5	10	3	...	...	...	2	22
Deep Bay*											
Mar. 1, 9	...	...	1	5	9	14	6	1	...	1	37
Cousins Inlet											
Jan. 13	6	1	...	2	1	...	...	...	...	...	10
Bella Bella											
Jan. 9, 11	4	4	11	13	5	...	...	...	...	...	37
Thompson Bay											
Jan. 6	...	...	1	1	5	...	...	...	...	...	7
Meyers Pass											
Dec. 15	1	15	5	1	...	...	...	...	...	...	22
Thistle Pass											
Dec. 16	3	15	7	3	...	...	...	...	...	...	28
Kitkatlah Inlet											
Jan. 21, 22, 30	5	...	8	40	9	1	...	...	...	...	63
Skidegate Inlet											
Dec. 6, 13, 14	12	5	15	3	...	...	...	...	...	...	35
Jan. 12, 30	29	...	2	1	...	...	...	...	...	...	32
Effingham Inlet											
Jan. 12	...	...	2	1	12	10	1	...	...	...	26
Quatsino Sound											
Dec. 6	1	16	13	5	...	...	...	...	...	...	35
Total	73	104	117	111	80	51	28	4	1	4	573

TABLE III. Arithmetic mean fecundity and mean body length, by age-groups. (Age-group II comprises fish approaching their second birthday, i.e. age I+.)

Locality	Age-group	Number of samples	Mean body length	Range in body length	Mean fecundity	Range in fecundity
			mm.	*mm.*		
Satellite Channel	II	3	169	158–178	10,913	9,230–12,742
	III	29	186	164–204	14,324	8,083–19,146
	IV	27	199	184–213	18,640	14,818–28,022
	V	6	208	200–217	22,972	17,134–28,675
	VI	1	215	...	23,627	...
Walker Rock	III	13	178	157–191	15,728	9,133–20,032
	IV	7	188	161–203	17,735	11,154–23,956
	V	8	205	188–222	18,198	12,352–24,838
Deepwater Bay	III	1	186	...	13,413	...
	IV	18	195	188–206	18,258	13,666–25,361
	V	11	206	193–219	24,402	16,133–32,906
	VI	4	219	214–227	26,680	21,719–34,043
	VIII	1	230	...	26,287	...
Effingham Inlet	II	1	160	...	8,238	...
	III	5	187	185–191	13,212	11,617–16,171
	IV	13	196	183–210	20,511	14,815–27,229
	V	4	207	204–213	24,468	21,671–29,622
	VI	2	217	211–222	24,758	22,070–27,446
	VII	1	220	...	27,072	...
Southern Group (4 samples combined)	II	4	166	158–178	10,244	8,238–12,742
	III	48	184	157–204	14,570	8,083–20,032
	IV	65	196	161–213	18,811	11,154–28,022
	V	29	206	188–222	22,404	12,352–32,906
	VI	7	218	211–227	25,695	21,719–34,043
	VII	1	220	...	27,072	...
	VIII	1	230	...	26,287	...
Fish Egg Inlet	III	6	176	166–185	14,810	10,108–18,781
	IV	48	188	170–205	21,123	10,993–37,659
	V	8	205	196–215	24,516	20,450–29,410
	VI	4	220	215–225	29,617	24,555–35,520
	VII	1	221	...	37,797	...
Bella Bella	III	2	174	165–182	13,503	11,699–15,308
	IV	20	193	167–212	20,662	10,555–31,941
	V	10	205	199–217	23,205	19,089–27,447
Thistle Pass	IV	18	194	173–206	19,164	14,607–24,325
	V	7	204	196–211	24,158	21,058–26,213
	VI	1	204	...	24,291	...
Meyers Pass	III	1	190	...	23,352	...
	IV	20	195	182–222	21,658	15,812–27,631
	VII	1	225	...	23,633	...
Kitkatlah Inlet	IV	35	194	180–217	20,129	14,897–29,140
	V	12	208	201–215	25,767	18,891–32,004
	VI	8	218	213–225	29,994	24,840–34,986
	VII	1	222	...	35,085	...

TABLE III. *Continued*

Locality	Age-group	Number of samples	Mean body length	Range in body length	Mean fecundity	Range in fecundity
			mm.	*mm.*		
Skidegate Inlet	IV	16	189	174–202	18,858	15,271–26,735
	V	6	210	192–225	24,925	16,987–31,439
	VI	4	222	207–242	37,715	29,829–54,185
	VII	1	229	...	59,064	...
Quatsino Sound	III	2	181	178–184	13,555	10,133–16,976
	IV	16	196	182–217	21,579	13,397–29,732
	V	12	214	195–229	27,624	18,290–34,262
	VI	2	214	213–214	28,650	26,916–30,384
	VII	1	222	...	32,262	...
	VIII	1	236	...	34,639	...
Northern Group (6 samples combined)	III	10	177	165–185	14,298	10,108–23,352
	IV	153	192	173–217	20,416	10,555–37,639
	V	45	207	192–225	24,695	16,978–34,262
	VI	19	218	204–242	31,098	24,291–54,185
	VII	4	223	221–229	41,052	23,633–59,064
	VIII	1	236	...	34,639	...

TABLE IV. Analysis of covariance of the multiple regression of log fecundity on log body length and log age. A double asterisk (**) indicates a difference which is significant at or beyond the 0.01 level of probability.

Samples tested	Source of variation	R^2	Errors of estimate: Degrees of freedom	Errors of estimate: Sums of squares	Errors of estimate: Mean square	F value
Quatsino Sd.–Fish Egg Inlet–Bella Bella–Thistle Pass–Kitkatlah Inlet–Skidegate Inlet	Total	0.6652	238	1.1948		
	Within samples	0.6595	233	1.1683	0.0050	
	Between samples	...	5	0.0265	0.0053	1.06
Satellite Ch.–Deepwater Bay–Walker Rock–Effingham Inlet	Total	0.6371	152	0.8192		
	Within samples	0.5965	149	0.7970	0.0053	
	Between samples	...	3	0.0222	0.0074	1.38
Combined northern sample–Satellite Channel	Total	0.6796	302	1.6707		
	Within samples	0.6705	301	1.4547	0.0048	
	Between samples	...	1	0.2160	0.2160	45.00**
Combined northern sample–Deepwater Bay	Total	0.6273	271	1.4882		
	Within samples	0.6462	270	1.4071	0.0052	
	Between samples	...	1	0.0811	0.0811	15.60**
Combined northern sample–Effingham Inlet	Total	0.6682	262	1.3661		
	Within samples	0.6744	261	1.3143	0.0050	
	Between samples	...	1	0.0518	0.0518	10.36**
Combined northern sample–Walker Rock	Total	0.6454	264	1.4789		
	Within samples	0.6262	263	1.4285	0.0054	
	Between samples	...	1	0.0504	0.0504	9.33**
Combined northern sample–combined southern sample	Total	0.6442	391	2.3400		
	Within samples	0.6469	390	2.0572	0.0053	
	Between samples	...	1	0.2828	0.2828	53.36**

TABLE V. The calculated geometric mean number of eggs in female herring in northern and southern British Columbia, by age-group and body length.

Age-group	Number of eggs in females of length (*mm.*)								
	160	170	180	190	200	210	220	230	240
					NORTHERN BRITISH COLUMBIA				
II	10200	12400	15000	...	...	...	...	...	...
III	10600	12900	15500	18500	21800	...	...	...	...
IV	10800	13200	15900	18900	22300	26200	...	...	...
V	...	...	16200	19300	22700	26600	31000	...	...
VI	...	...	...	...	23000	27000	31400	36300	41700
VII	...	...	...	...	...	27400	31800	36800	42200
VIII	...	...	...	...	...	...	32200	37200	42700
					SOUTHERN BRITISH COLUMBIA				
II	9300	10700	12100	...	...	...	...	...	...
III	10600	12200	13800	15500	17300	...	...	...	...
IV	11600	13400	15100	17000	19000	21100	...	...	...
V	...	...	16300	18300	20400	22700	25100	...	...
VI	...	...	...	...	21700	24100	26600	29300	32200
VII	...	...	...	...	...	25300	28000	30800	33800
VIII	...	...	...	...	...	...	29200	32200	35300

TABLE VI. The relation between log fecundity and log body length in each sample.

Locality	No. of fish	Regression coefficient, *b*	Intercept log C
Skidegate Inlet	30	3.558	−3.822
Kitkatlah Inlet	59	3.355	−3.368
Thistle Pass	28	2.453	−1.317
Bella Bella	34	3.469	−3.635
Fish Egg Inlet	70	3.600	−3.916
Quatsino Sound	35	3.597	−3.937
Deepwater Bay	36	2.933	−2.448
Walker Rock	29	1.769	+0.197
Satellite Channel	71	3.303	−3.334
Effingham Inlet	26	4.006	−4.913

TABLE VII. Analysis of covariance of the regression of log fecundity on log body length. Single and double asterisks indicate differences significant at the levels 0.05–0.01, and < 0.01, respectively.

	Average log fecundity adjusted to common log body length					Slope—rate of increase of log fecundity with log body length				
		Errors of estimate					Errors of estimate			
Samples tested	Source of variation	Degrees of freedom	Sum of squares	Mean square	F Value	Source of variation	Degrees of freedom	Sum of squares	Mean square	F Value
Skidegate Inlet–Kitkatlah Inlet–Fish Egg Inlet–Bella Bella–Thistle Pass–Quatsino Sound	Total	254	1.244255	...		Within samples	249	1.210685	...	
	Within samples	249	1.210685	0.004887		From individual samples	244	1.196014	0.004902	
	Between samples	5	0.033570	0.006714	1.37	Among sample regressions	5	0.04671	0.002934	0.60
Northern group–Deepwater Bay	Total	290	1.555661	...		Within samples	289	1.467119	...	
	Within samples	289	1.467119	0.005077		From individual samples	288	1.462319	0.005077	
	Between samples	1	0.088542	0.088542	17.42**	Among sample regressions	1	0.004800	0.004800	0.95
Northern group–Satellite Channel	Total	325	1.928864	...		Within samples	324	1.538773	...	
	Within samples	324	1.538773	0.004749		From individual samples	323	1.538149	0.004762	
	Between samples	1	0.390091	0.390091	82.14**	Among sample regressions	1	0.000624	0.000624	0.13
Quatsino Sound–Effingham Inlet	Total	59	0.279081	...		Within samples	58	0.260293	...	
	Within samples	58	0.260293	0.004488		From individual samples	57	0.258649	0.004538	
	Between samples	1	0.018788	0.018788	4.18*	Among sample regressions	1	0.001644	0.001644	0.36
Deepwater Bay–Satellite Channel	Total	105	0.536802	...		Within samples	104	0.508902	...	
	Within samples	104	0.508902	0.004893		From individual samples	103	0.506644	0.004919	
	Between samples	1	0.027900	0.027900	5.70*	Among sample regressions	1	0.002258	0.002258	0.46
Satellite Channel–Effingham Inlet	Total	95	0.439321	...		Within samples	94	0.420332	...	
	Within samples	94	0.420332	0.004472		From individual samples	93	0.412436	0.004435	
	Between samples	1	0.018989	0.018989	4.25*	Among sample regressions	1	0.007896	0.007896	1.78
Satellite Channel–Walker Rock	Total	98	0.517784	...		Within samples	97	0.491908	...	
	Within samples	97	0.491908	0.005071		From individual samples	96	0.436442	0.004546	
	Between samples	1	0.025876	0.025876	5.10*	Among sample regressions	1	0.055466	0.055466	12.20**

A Comparison of Sockeye Salmon Catches at Rivers Inlet and Skeena River, B.C., with Particular Reference to Age at Maturity[1]

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ABSTRACT

Age composition, size and sex data for sockeye salmon catches (1912–1954) at Rivers Inlet and Skeena River, B.C. were compared. For both river systems there were indications of 4- and 5-year cycles of abundance among the 4- and 5-year-old fish, respectively; but the two populations were not necessarily in phase. Tests for correlation between the numbers of parental and offspring fish strongly suggested the dominance of hereditary over environmental influence in determining age at maturity. The two stocks showed much similarity in annual size variation, among each sex and age-class.

INTRODUCTION

Forty-three years of age composition data of Rivers Inlet and Skeena River sockeye salmon (*Oncorhynchus nerka*) catches have shown that although several age-classes are present in the runs, fish which are approaching 4 and 5 years of age, respectively, and which migrated to sea in their second year of life (therefore described as 4_2 and 5_2 fish) have made up the great bulk of the adult returns. At Rivers Inlet they have averaged about 98% of the catches, and at Skeena River roughly 90%. At the same time, however, there has been considerable year-to-year variation in the proportions of these age-classes that appear in the annual runs. This irregularity in the proportionate production of the two major age-classes has contributed to the difficulty of understanding the causes of changes in abundance of sockeye salmon populations, and of predicting the times and magnitudes of adult returns. There is need for determining in what way, and to what degree, hereditary factors and/or environmental conditions are responsible for influencing the rate of maturing of sockeye, and, therefore, the age at which they return. If *environmental* conditions were primarily responsible for determining age at maturity, then it could be expected that apparently random and (at present) unpredictable fluctuations would characterize the changes in abundance of the different age-classes among the returning adults. On the other hand, if *hereditary* factors are of major importance in governing the age of return, then the fluctuations in abundance of different age-classes would tend to follow predictable patterns, and levels of abundance of particular age-groups would tend to be stable (apart from fluctuations caused by variations in survival rates).

The spawning systems of Rivers Inlet and Skeena River are widely separated geographically, and there are great differences in their physical characteristics.

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If, therefore, *both* systems exhibited patterns of abundance of stock that are suggestive of hereditary control of age at maturity, then the evidence of such control would be strengthened. Similarly, evidence of environmental control of age at maturity would be supported if the two systems exhibited parallel "random" fluctuations in abundance of the two ages.

The mouth of the Skeena lies almost 200 miles north of Rivers Inlet, along the coast, and the two systems are separated by roughly 2½ degrees of latitude. Rivers Inlet spawning streams are few in number and lie at relatively very short distances from the sea. They all feed into a single nursery lake for the young sockeye. The Skeena River, on the other hand, transects the range of coastal mountains, and in the central plateau west of the Continental Divide separates into three main branches. These continue far inland (roughly in northerly, easterly and southeasterly directions), and each has its own system of nursery lakes. The area of the Rivers Inlet watershed (Wannock) is given as 1,618 square miles, whilst that of the Skeena is 21,038 square miles (Gazetteer of Canada, British Columbia, 1953).

The climate of the Rivers Inlet spawning region is typically coastal, with very high annual precipitation, and moderate temperatures. That of most of the Skeena is characteristic of the central plateau, where rainfall is usually moderate, and the temperature often extreme.

MATERIAL USED

Data on the age composition of the *total* sockeye stocks of the two river systems are not available, since there is no information on the age composition of escapements. These analyses have therefore depended upon age composition data, available since 1912, of the annual sockeye catches at Rivers Inlet and Skeena River. It has been necessary to make the assumption that, to a reasonable degree, the age composition of the catches is representative of the total adult returns. Although this is not strictly correct, mainly because of the selective action of the commercial gill nets for size (and therefore for age and sex, also), it is possible that the original proportions of the different age-classes that appear in the total returns are retained without major alteration, in catch and escapement. In any event, it is suggested that if differences do occur, they are not great enough to mask the obvious and marked trends in abundance that have taken place, which form the basis for certain of the following comparisons.

The data that have been used have been published annually in "The Report of the British Columbia Department of Fisheries" under the series, "Contributions to the life history of the sockeye salmon". These have included contributions by C. H. Gilbert (for 1912–1924), W. A. Clemens (for 1925–1948), and D. R. Foskett (for 1949–1954).

The catches reported are the number of 48-lb. cases of sockeye salmon packed each year. The age composition of the catch was determined on the basis of periodic sampling throughout the fishing season at one of the major canneries,

which, in general, was fairly proportional to the landings there. The total packs were divided into the approximate numbers of 4-year and 5-year fish caught, by allowing that approximately 72 lb. of fish meat are used in a 48-lb. case of canned sockeye, and computing on the basis of the published annual average weight of each sex in each age-class (Tables I and II).

Because the great majority of sockeye caught at Rivers Inlet and Skeena River have been the 4_2 and 5_2 fish, only these two age-classes have been used in the comparisons. When reference is made to *peak* catches, they will be those that are higher than ones of the immediately preceding and succeeding years.

TABLE I. Rivers Inlet annual sockeye packs, and estimated catches of numbers of 4_2 and 5_2 fish.

Year of catch	Pack	Av. weight per fish	Estimated 1,000's of fish	Percent 4_2's	Percent 5_2's	Estimated 1,000's of 4_2 fish	Estimated 1,000's of 5_2 fish
	cases	*pounds*					
1912	112,884	6.6	1,231	21	79	259	973
1913	61,745	5.7	780	80	20	624	156
1914	89,890	6.4	1,011	35	65	354	657
1915	130,350	6.69	1,403	13	87	182	1,220
1916	44,936	...	536	26	74	139	397
1917	61,195	...	689	39	61	269	420
1918	53,401	5.62	684	57	43	390	294
1919	56,258	5.52	734	46	54	338	396
1920	121,254	6.78	1,288	5	95	64	1,223
1921	46,300	5.92	563	49	51	276	287
1922	60,700	6.19	706	81	18	572	127
1923	107,174	5.22	1,478	74	24	1,094	355
1924	94,891	5.64	1,211	43	54	521	654
1925	159,554	5.99	1,918	23	77	441	1,477
1926	65,581	5.72	825	59	38	487	314
1927	64,461	5.80	800	81	16	648	128
1928	60,044	5.73	754	55	40	415	302
1929	70,260	5.28	958	77	18	738	172
1930	119,170	5.97	1,437	49	48	704	690
1931	76,428	5.45	1,010	53	44	535	444
1932	69,732	5.22	962	67	27	644	260
1933	83,507	5.89	1,021	44	55	449	561
1934	76,923	5.22	1,061	77	20	817	212
1935	135,038	5.28	1,841	57	41	1,050	755
1936	46,351	5.60	596	53	46	316	274
1937	84,832	5.05	1,209	60	37	726	448
1938	87,942	6.08	1,041	27	70	281	729
1939	54,143	4.90	796	67	32	533	255
1940	63,469	5.53	826	69	28	570	231
1941	93,378	4.94	1,361	59	40	803	544
1942	79,199	6.56	869	8	91	70	791
1943	47,602	6.29	545	8	91	44	496
1944	36,852	4.89	543	76	23	412	125
1945	89,735	5.25	1,231	57	41	701	505
1946	73,320	5.58	946	37	63	350	596
1947	140,087	6.02	1,675	3	97	50	1,625
1948	37,665	5.83	465	55	44	256	205
1949	39,495	4.59	619	84	14	520	87
1950	142,710	6.45	1,593	13	87	207	1,386
1951	102,565	6.73	1,097	38	60	417	658
1952	84,298	6.59	921	41	58	378	534
1953	132,925	5.58	1,715	73	26	1,252	446
1954	50,639	6.25	588	60	39	353	229

TABLE II. Skeena River annual sockeye packs, and estimated catches of numbers of 4_2 and 5_2 fish.

Year of catch	Pack	Average weight per fish	Estimated 1,000's of fish	Percent 4_2's	Percent 5_2's	Estimated 1,000's of 4_2 fish	Estimated 1,000's of 5_2 fish
	cases	*pounds*					
1912	92,498	6.08	1,095	57	43	624	471
1913	52,927	5.85	651	50	50	326	326
1914	130,166	6.43	1,458	25	75	364	1,093
1915	116,553	6.12	1,371	36	64	494	878
1916	60,923	...	706	34	38	240	268
1917	65,760	...	863	57	29	492	250
1918	123,322	5.95	1,492	51	34	761	507
1919	184,945	6.34	2,100	27	60	567	1,260
1920	90,869	6.43	1,018	15	71	153	722
1921	41,018	5.52	534	69	22	368	117
1922	96,277	5.40	1,284	70	16	899	205
1923	131,731	5.40	1,756	56	29	984	509
1924	144,747	6.22	1,676	23	69	385	1,156
1925	77,784	5.47	1,024	51	45	522	461
1926	82,360	5.49	1,080	62	26	670	281
1927	83,996	5.49	1,102	62	28	683	308
1928	34,559	5.32	468	51	39	239	182
1929	78,017	5.37	1,046	62	30	649	314
1930	132,372	5.87	1,624	39	52	633	844
1931	93,023	5.64	1,188	40	30	475	356
1932	59,916	5.82	741	44	37	326	274
1933	30,506	5.52	398	57	36	227	143
1934	54,558	6.01	654	58	34	379	222
1935	52,879	5.61	679	49	31	333	210
1936	81,973	5.73	1,030	67	20	690	206
1937	42,491	5.39	568	45	40	255	227
1938	47,257	5.25	648	64	15	415	97
1939	68,485	5.27	936	50	35	468	327
1940	116,507	5.62	1,493	80	15	1,194	224
1941	81,767	5.71	1,031	39	52	402	536
1942	34,544	5.65	440	36	54	158	238
1943	28,268	5.44	374	39	39	146	146
1944	68,197	5.74	855	37	52	317	445
1945	104,279	5.93	1,266	20	63	253	798
1946	52,928	5.91	645	13	70	84	451
1947	32,534	5.97	392	14	82	55	322
1948	101,267	5.37	1,358	80	13	1,086	177
1949	65,937	6.19	767	17	76	130	583
1950	47,479	6.0	570	21	72	120	410
1951	61,694	6.2	716	33	61	236	437
1952	114,775	5.8	1,425	66	26	940	370
1953	65,003	6.4	731	48	43	351	314
1954	60,817	6.6	663	33	54	219	358

ANNUAL CATCHES, 1912–1954

Annual catches of 4_2 and 5_2 sockeye at Rivers Inlet and Skeena River are shown in Figures 1 and 2, respectively; the two systems are compared in Figure 3. (See also Table I and II.)

The combined catch of the two age-groups has shown large fluctuations, but whereas the average catch for Rivers Inlet has been fairly constant during 1912–1945 (roughly 1 million sockeye per annum), that of Skeena declined during 1915–1930 approximately (from about 1 million to something over half a million per annum), after which it experienced a slight increase.

In both systems the average catch of 4_2 fish has remained relatively constant, and so has the average catch of 5_2 fish at Rivers Inlet. At Skeena River the average

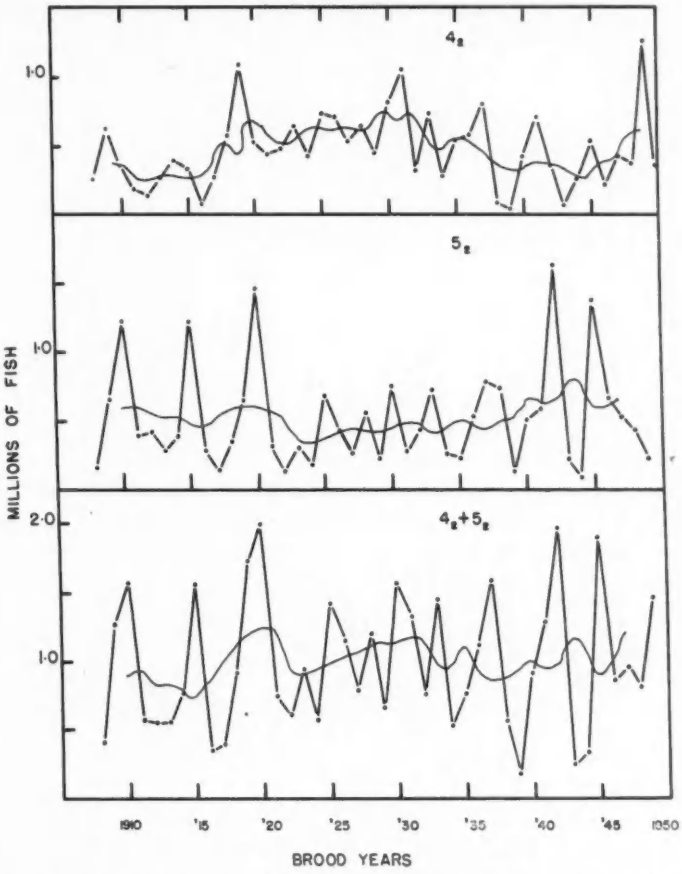

FIG. 1.—Annual (brood-year) catches of 4_2 and 5_2 sockeye at Rivers Inlet. (Thin line is running average of 5's.)

catch of 5_2 fish declined during 1915–1930, and then showed some increase. The changes in the 5_2 catches contributed most to the observed changes in the combined Skeena catch.

In both systems peak catches of 4_2 and 5_2 fish have gone as high as 2 million fish, while low catches have been as little as about 300,000 fish. High catches of 5_2 fish have exceeded 1 million sockeye, and low catches have, on occasions, been below 200,000 sockeye, in both fisheries. Among 4_2 fish, in both fisheries, high catches have at times exceeded 1 million sockeye, and small catches have been less than 100,000 sockeye.

Apparent "cycles" of abundance (line-dominance) have occurred at both systems. Thus, among the 5_2 sockeye, there were peak catches separated by

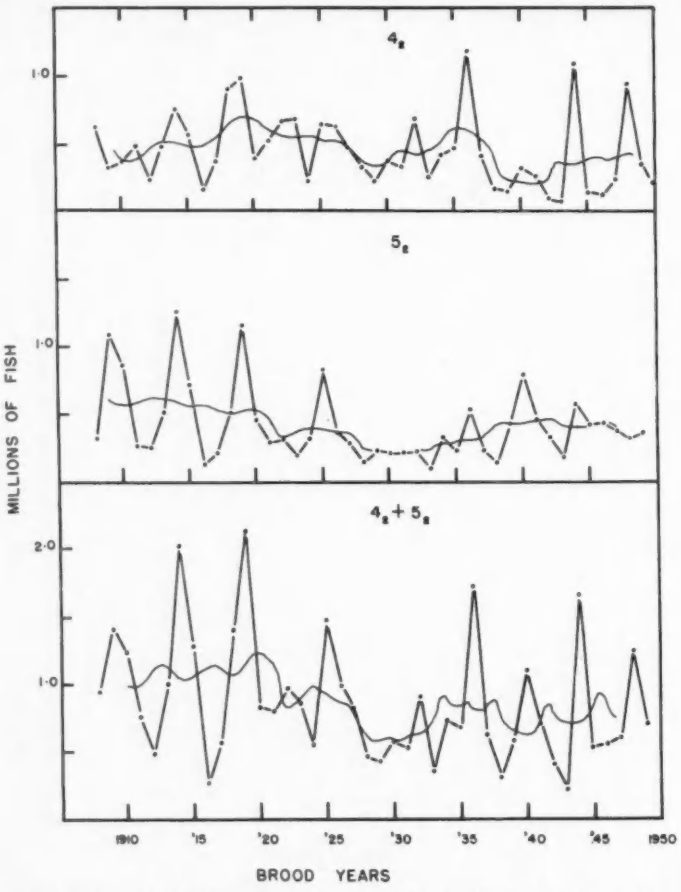

FIG. 2.—Annual (brood-year) catches of 4_2 and 5_2 sockeye at Skeena River. (Thin line is running average of 5's.)

5-year intervals in the brood years 1910, 1915, 1920, 1925 and 1930, for Rivers Inlet; and in 1909, 1914 and 1919, for Skeena River. Among 4_2 fish of Rivers Inlet there were peak catches separated by 4-year intervals in 1933, 1937, 1941, 1945 and 1949; and of Skeena River, in 1932, 1936, 1940, 1944 and 1948. During the early third of the 1908–1950 (brood years) period, when an apparent 5-year cycle persisted, there is no evidence of a 4-year cycle among 4-year fish; and, conversely, when later the 4-year cycle among 4-year fish occurred, there was no definite 5-year cycle among 5-year fish.

The two systems have thus shown several points of similarity in their annual catches. These were: (a) the magnitudes of high and low catches of both age-

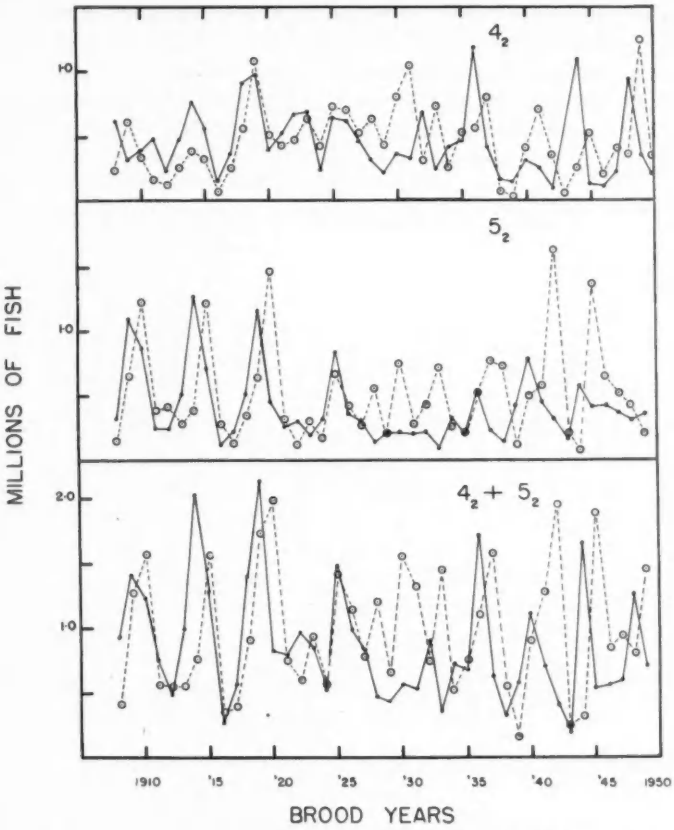

FIG. 3.—Comparisons between Rivers Inlet (broken line) and Skeena River (solid line) catches of 4_2 and 5_2 sockeye.

classes; (b) the 5-year cycle among 5-year fish, early in the 1912–1954 period, and the 4-year cycle among 4-year fish, in the latter part of that period; (c) in both systems fluctuations among 5_2 fish were usually much greater than among 4_2 fish; as a result, changes in the total annual catch to a great extent reflect changes in the abundance of 5_2 fish rather than 4_2 fish.

Although both very high and very low catches at Rivers Inlet and Skeena River have been quite similar in magnitude, they usually have not occurred simultaneously. Frequently they took place with a difference between the two systems of one year. This difference, and the apparent cyclic character of the returns in each age-class, appear to constitute a kind of predictable pattern (rather than mere random fluctuation), suggestive of control over the abundance of a particular age-class that is not mainly environmental.

RATIOS OF 5_2 TO 4_2 FISH CAUGHT

Although the proportions of 5_2 and 4_2 fish of the same brood-year stocks have shown considerable year-to-year variation, they have also experienced certain fairly distinct trends. The 5_2:4_2 ratios (of fish of the same brood-year stocks) are shown in Figures 4 and 5 for Rivers Inlet and Skeena River, respectively; and the two systems are compared in Figure 6.

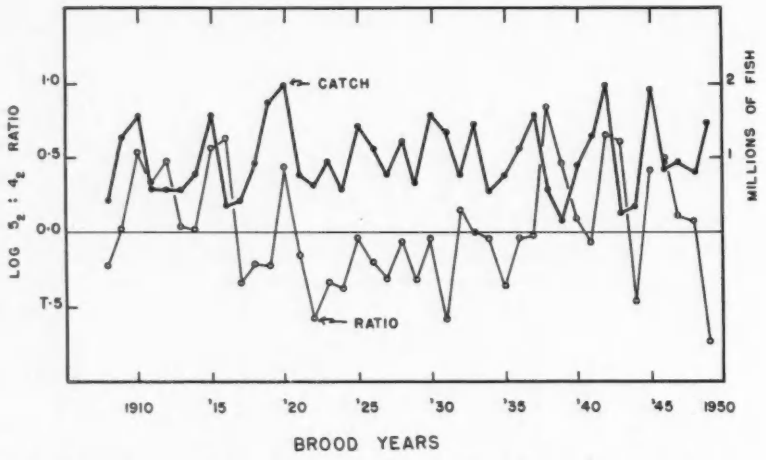

FIG. 4.—Rivers Inlet—the log of the 5_2:4_2 ratio in annual catches, and the combined catch of 4_2 and 5_2 sockeye, of fish of the same brood-year stocks.

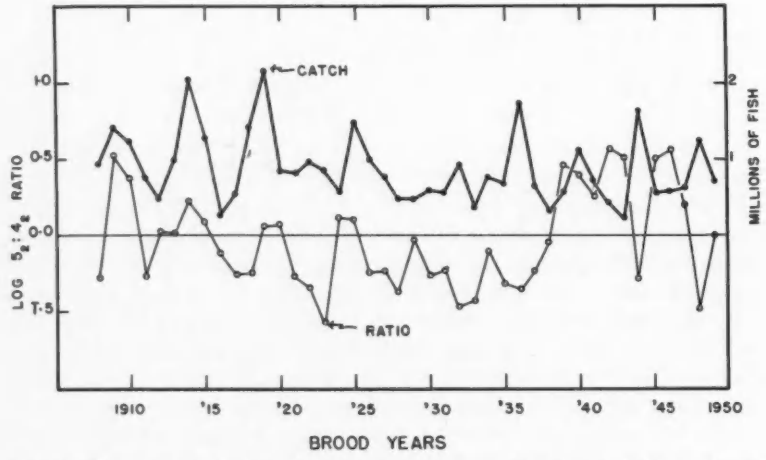

FIG. 5.—Skeena River—the log of the 5_2:4_2 ratio in annual catches, and the combined catch of 4_2 and 5_2 sockeye, of fish of the same brood-year stocks.

Three fairly distinct periods are evident in both systems; an early period (roughly the brood years 1908–1920), when 5_2 fish usually dominated the catches, and when both the ratio and the combined catch showed marked fluctuations; a central period (brood years 1920–1936), when 4_2 fish usually dominated the catches, and when both ratio and combined catch were more constant; and a late period (brood years 1936–1950), when again the 5_2:4_2 ratio was often high, and when the combined catch showed large variations.

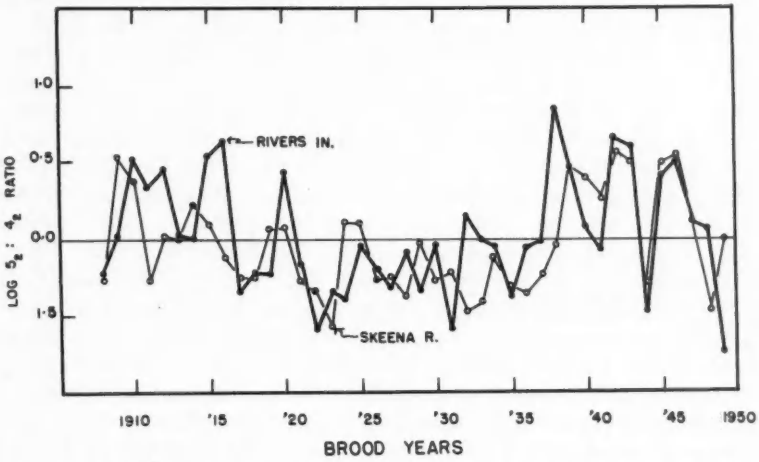

FIG. 6.—Comparison between Rivers Inlet and Skeena River of the 5_2:4_2 log ratios in annual sockeye catches.

The average catches, in thousands of 4_2 and 5_2 fish during the early, central and late brood-year periods were as shown:

Fishery	Age	Early period	Middle period	Late period	Total
Rivers Inlet	5_2	590	385	588	516
	4_2	391	586	431	471
Ratio	5_2:4_2	1.51:1	0.65:1	1.36:1	1.10:1
	Combined	981	971	1.019	990
Skeena River	5_2	588	281	399	418
	4_2	512	464	391	449
Ratio	5_2:4_2	1.15:1	0.61:1	1.02:1	0.93:1
	Combined	1,100	745	790	873

Differences between the average catches of 4_2 plus 5_2 fish, when one or the other age-class dominated the catches, were not very great. For the entire brood-year period of 1908–1949, catches at Rivers Inlet have been 21.2 million 5_2 fish, and 20.2 million 4_2 fish; and at Skeena River, 17.6 million 5_2 fish, and 19.3 million 4_2 fish. Combined catches of 4_2 and 5_2 fish have amounted to almost 42 million at Rivers Inlet, and 37 million at Skeena River.

In both fisheries, over the whole of the period of brood years 1908–1949, the numbers of 4_2 and 5_2 fish caught have been quite similar. (In the actual sampling data the proportions were: at Rivers Inlet, among a total sample of 55,000 sockeye of these ages, 51% were 5_2 and 49% were 4_2 fish; at Skeena River, among a total sample of 70,000 sockeye, 48% were 5_2 fish and 52% were 4_2 fish.)

CORRELATIONS BETWEEN CATCHES OF PARENTAL AND PROGENY STOCKS

Whether age at maturity is governed by hereditary or environmental influences, or both, may be examined by means of the correlation method. In general, the tests which follow are similar to those used by Milne (1954) for Skeena catches, the differences here being: (a) only 4_2 and 5_2 fish are considered; (b) the catch in cases was transformed to numbers of fish, making allowance for weight differences between sex and age-class; (c) Milne's method of adjusting for trends in catches was not used[2]; (d) to reduce the effects of trends and of larger annual fluctuations, the catches were first transformed to logarithms; (e) additional correlations have been computed to test the several hypotheses.

The opportunity of comparing the results for two river systems has been useful in arriving at firmer conclusions.

The hypotheses depend upon the assumption that annual samples were adequately (not necessarily perfectly) representative of the age composition of the total returns. Three hypotheses are presented below, and each is followed by one or more corollaries that serve to define the useful statistical tests. In some cases the validity of a corollary also depends upon an additional assumption, in which case that assumption is given before the corollary or corollaries in question.

The several correlations determined are listed in Table III. "Significance" of correlations (the probability that they differ from zero) was obtained directly from Table 7.3 of Snedecor (1946), and the significance of the difference between correlations was computed using the "z" transformation (Fisher, 1950, p. 203; and Fisher and Yates, 1949, Table VII).

Hypothesis 1.

Age at maturity is determined solely by heritable genetic factors. (Either the 4_2 and 5_2 fish might breed separately; or, breeding together, progeny age could be determined by a genetic mechanism which is assumed to have reached

[2]The Rivers Inlet catches show practically no trend throughout the period considered (Fig. 1). However, on the Skeena the catches at first declined, later increased a little; and this means that catches only 4 or 5 years apart tend to be more alike than more distantly separated years, quite apart from, and in addition to, any parent-progeny similarity. To assess the magnitude of this effect upon the correlations, a straight line was fitted to the sequence of logarithms of catches, and "Correlation A" (see Table III) was computed from the "residuals" (regression values less actual values). The figure obtained was 0.498, as compared with 0.543 from the unadjusted data. Generally similar decreases would be expected with all the other correlations in Table III, but none of the highly significant "*r*" values would thereby be reduced to below the $P = 0.01$ level, and *comparisons* of correlations would scarcely be affected at all. Thus none of the arguments below would be altered by adjustments for the trend. The generally larger magnitude of correlations for the Skeena, in Table III, as compared with Rivers Inlet, is likely mainly the result of the catch trends in the former area.

equilibrium, in the sense that the eggs laid by a given breeding stock would reproduce the 4_2:5_2 ratio of their parents *if* all survived to maturity. In the latter event actual variations in the 4_2:5_2 ratio among maturing fish of a given brood would be the result of year-to-year differences in survival rate among the two types, one of which must live a year longer in the ocean than the other.)

A *supplementary assumption* is that over the range of escapements involved here, there is a fairly large positive correlation between abundance of spawning stock and the number of progeny which it produces.

COROLLARIES, AND RESULTS OF TESTS FOR CORRELATION

(a) There should be a positive correlation between number of 4_2 fish in year n and number of 4_2 fish in year $n + 4$ (Correlation A).

Results: Correlation A is positive and significant; $P < .05$ (Rivers Inlet), and $< .01$ (Skeena River).

(b) There should be a positive correlation between number of 5_2 fish in year n and 5_2 fish in year $n + 5$ (Correlation B).

Results: Correlation B is positive and significant; $P < .01$ (Rivers Inlet), and $< .01$ (Skeena River).

(c) There should be zero correlation (within limits of sampling error) between number of 5_2 fish in year n and number of 4_2 fish in year $n + 4$ (Correlation C).

Results: (1) Correlation C is not significantly different from zero; $P = 0.696$ (Rivers Inlet), and 0.273 (Skeena River). (2) Correlation C is negative for Rivers Inlet, and positive for Skeena River.

(d) There should be zero correlation (within limits of sampling error) between number of 4_2 fish in year n and number of 5_2 fish in year $n + 5$ (Correlation D).

Results: (1) Correlation D is not significantly different from zero; $P = 0.118$ (Rivers Inlet), and 0.425 (Skeena River). (2) Correlation D is negative for Rivers Inlet, and positive for Skeena River.

(e) There should be positive correlation, less than correlation B, between number of 4_2 plus 5_2 fish in year n and number of 5_2 fish in year $n + 5$ (Correlation J).

Results: Correlation J is positive and significant for both rivers, but is less than each corresponding Correlation B.

(f) There should be positive correlation, less than Correlation A, between number of 4_2 plus 5_2 fish in year n and number of 4_2 fish in year $n + 4$ (Correlation K).

Results: Correlation K is positive and significant; for Rivers Inlet it has almost the same value as Correlation A, and for Skeena River it is slightly less than Correlation A. However, the sampling error of the correlations is such that the population value of Correlation K may well be appreciably less than that of Correlation A.

(g) Correlations A and B would be large (would approach the value indicated in the supplementary assumption above), if environmental factors affecting

reproductive success were invariable from year to year. If, in addition, percentage reproductive success were independent of density of spawners, these correlations would be unity. Since environmental factors affecting success actually vary considerably from year to year, Correlations A and B would likely be much less than they would be otherwise; however, environmental factors probably affect 5_2 and 4_2 fish equally. Hence, Correlations A and B should be approximately the same.

Results: Correlations A and B do not differ significantly from each other, for both rivers; P = 0.238 (Rivers Inlet), and 0.534 (Skeena River).

(h) There would be no correlation between number of 4_2 fish in year n and number of 5_2 fish in year $n + 1$ (since the ratio of 5_2's to 4_2's in a filial generation would always be the same as in the parental stock), *except for the fact* that the two groups hatched in the same year and lived for 3½ years under similar environmental conditions, and the environment presumably varies from year to year. Therefore, for this reason there could be a weak to moderate positive correlation between number of 4_2 fish in year n and number of 5_2 fish in year $n + 1$ (Correlation G.)

Results: Correlation G is positive and not very large, being 0.300 for Rivers Inlet, and 0.358 for Skeena River. Neither figure is significant, but with the number of observations available a small correlation cannot be proven, even if it actually exists.

General conclusion. The above results are all consistent for Hypothesis 1 and its corollaries, and with the possible exception of corollary (f), they all may be said to support it. Hence, the hypothesis cannot be rejected, although it is not necessarily proven.

Table III. Correlations (r) between catches ($\log_{10}$ numbers of fish) of parental and progeny stocks of sockeye salmon at Rivers Inlet and Skenna River, 1912–1954. An asterisk denotes a statistically significant relationship.

		Rivers Inlet			Skeena River		
Parent	Offspring	No. of years	r	P	No. of years	r	P
A. 4_2 in year n	4_2 in year n+4	39	+0.388*	<.05	38	+0.543*	<.01
B. 5_2 in year n	5_2 in year n+5	37	+0.599*	<.01	37	+0.640*	<.01
C. 5_2 in year n	4_2 in year n+4	38	−0.066	>.05	38	+0.183	>.05
D. 4_2 in year n	5_2 in year n+5	38	−0.258	>.05	38	+0.134	>.05
E. 4_2 plus 5_2 in year n	4_2 in year n+4 plus 5_2 in year n+5	38	+0.394*	<.05	38	+0.617*	<.01
F. 4_2 in year n+4 plus 5_2 in year n+5	4_2 plus 5_2 in year n	38	+0.167	>.05	38	+0.453*	<.01
G. 4_2 in year n	5_2 in year n+1	40	+0.300	>.05	42	+0.358*	<.05
J. 4_2 plus 5_2 in year n	5_2 in year n+5	38	+0.409*	<.05	38	+0.536*	<.01
K. 4_2 plus 5_2 in year n	4_2 in year n+4	38	+0.390*	<.05	38	+0.516*	<.01

Hypothesis 2

The genetic make-up of any fish, insofar as it affects the age at which it matures, is independent of the age of its parents. Variations between broods in

age at maturity, if they exist, are determined solely by variation in environmental factors.

The *supplementary assumption* is the same as for Hypothesis I.

COROLLARIES, AND RESULTS OF TESTS FOR CORRELATION

(a) Correlations A and D should both be positive, and should be approximately equal: If age at maturity of progeny is independent of the age of the parents, then age 4_2 parents in year n should produce both 4_2 progeny in year $n + 4$, and 5_2 progeny in year $n + 5$. Thus, Correlations A and D should both be positive. Since the two age-classes so produced would have experienced similar environmental conditions for the first 3½ years of life, the relationship between 5_2 progeny in year $n + 5$ to 4_2 parents in year n should be very similar to that between 4_2 progeny in year $n + 4$ and 4_2 parents in year n. Thus, Correlations A and D should be approximately equal.

Results: Correlations A and D are significantly unequal for both rivers; $P = 0.002$ (Rivers Inlet), and 0.048 (Skeena River). Also, Correlation D for Rivers Inlet is negative.

(b) Correlations B and C should both be positive, and should be approximately equal, for reasons similar to (a) above.

Results: Correlations B and C are significantly unequal for both rivers; $P = 0.002$ (Rivers Inlet), and 0.017 (Skeena River). Furthermore, Correlation C for Rivers Inlet is negative.

(c) Correlation E should be positive, and since it has the whole spawning stock for one variate, should be substantially greater than each of Correlations A, B, C and D.

Results: Correlation E is positive, for both rivers, but is not greater than *each of* A, B, C and D: it is less than Correlation B and not significantly greater than A.

(d) Correlations B, D and J should be positive. If age at maturity is independent of the age of the parents, then 5_2 progeny in year $n + 5$ should be positively correlated with both 4_2 and 5_2 parents in year n (Correlations B and D), and with the sum of the 4_2 and 5_2 parents in year n (Correlation J). Also, if 4_2 and 5_2 fish tend to be of about equal abundance on the average (as they appear to have been), Correlations B and D should be about equal.

Results: Correlations B and J are positive for both rivers; Correlation D is positive for Skeena River, but is negative for Rivers Inlet. Also, Correlations B and D are significantly different; $P < 0.0001$ (Rivers Inlet), and < 0.01 (Skeena River).

(e) Correlation J, since it has the whole spawning stock for one variate, should exceed both Correlations B and D.

Results: Correlation J does not exceed *both* of Correlations B and D (for both rivers, it is smaller than Correlation B).

(f) Correlations A, C and K should be positive. For reasons similar to those given under (d) above, 4_2 progeny in year $n + 4$ should be positively correlated

with both 4_2 and 5_2 parents in year *n* (Correlations A and C), and with the sum of the 4_2 plus 5_2 parents in year *n* (Correlation K). Also, Correlations A and C should be about equal.

Results: Correlations A and K are positive, for both rivers; Correlation C is positive for Skeena River, but is negative for Rivers Inlet. Also, for both rivers, Correlations A and C are different; the difference is statistically "significant" at Rivers Inlet ($P = 0.046$), and "suggestive" at Skeena River ($P = 0.077$).

(g) Correlation K, since it has the whole spawning stock as one variate, should exceed both Correlations A and C.

Results: Correlation K, for Rivers Inlet, does exceed both Correlations A and C, but is obviously not significantly different from Correlation A. Correlation K, for Skeena River, does not exceed both Correlations A and C, but it is not significantly different from Correlation A.

(h) Correlations J and K should be approximately equal, for reasons similar to those given under (d) above.

Results: Correlations J and K are not significantly different: $P = 0.923$ (Rivers Inlet), and 0.904 (Skeena River).

(i) In addition to being greater than Correlations A, B, C and D (see (c) above), Correlation E should be greater than both Correlations J and K, since it has both the whole spawning stock and the whole progeny stock as variates.

Results: Correlation E is greater than Correlations J and K, except for Rivers Inlet Correlation J, from which it does not differ significantly ($P = 0.94$).

(j) Correlation G could have almost any value. Correlations between the numbers of progeny of the two age-classes produced from the same brood-year stocks (that is, between 4_2 fish in year *n* and 5_2 fish in year $n + 1$, as in this correlation) may be either positive or negative. Since both kinds of young were hatched in the same year, and for about 3½ years were exposed to the same environmental conditions, their survival rates should be more alike than those of fish hatched in different years. This would tend to make for a positive correlation. On the other hand, at the time of segregation into the 4_2 and 5_2 groups, any environmental factor favouring excess of 4_2 fish would automatically reduce the numbers of 5_2 fish, and vice versa; this effect, by itself, would produce a negative correlation.

Results: Since almost any value of correlation would be consistent with this proposition, it is not considered further.

GENERAL CONCLUSION. Since most of the corollaries to Hypothesis 2 do not conform with the appropriate tests, it cannot be accepted.

HYPOTHESIS 3

Age at maturity is determined partly by parental age, and partly by variations in environmental influences. (The environmental factors usually suggested are those affecting rate of growth of the fish; for example, that the faster the sockeye grow, the more of them will mature at an earlier age. Although the average growth rate of earlier-maturing sockeye is greater than that of later-maturing fish of the same brood, this, in itself, does not establish that rate of growth affects

age at maturity; fish may, or may not inherit factors for slower growth and consequently for later maturing).

The *supplementary assumption* is the same as for Hypotheses 1 and 2.

COROLLARIES, AND RESULTS OF TESTS FOR CORRELATION

In general, the corollaries for Hypothesis 3 would be intermediate between those for Hypotheses 1 and 2.

(a) Correlations A, B, C and D should all be positive, but Correlations A and B should be greater than Correlations C and D.

Results: Correlations A and B are positive, for both rivers. Correlations C and D are positive and smaller than Correlations A and B, for Skeena River, and are weakly negative for Rivers Inlet. Thus, the Skeena fish do not contradict Hypothesis 3. The Rivers Inlet fish would contradict the hypothesis if the negative values of Correlations C and D were significant. However, they are not; and their limits of error (for $P = 0.05$) go as high as 0.068 for Correlation D, and 0.259 for Correlation C, so that it cannot be concluded definitely that all environmental influence is rejected.

(b) Correlations A and B should be nearly equal, as should also Correlations C and D.

Results: Correlations A and B, and Correlations C and D are close enough to equal (both rivers) to comply with the hypothesis.

(c) Correlation G, as explained under Hypothesis 2, could be either positive or negative. However, whereas a positive value would be inconclusive, a significant negative value would prove some environmental effect upon age at maturity.

Results: Correlation G is positive, for both rivers, and cannot, therefore, contribute to a test of the hypothesis.

GENERAL CONCLUSION. Hypothesis 3 cannot be rejected.

INTERPRETATION

The results of these tests are interpreted as indicating that very definitely age at maturity in sockeye salmon is governed to a great extent by the inheritance of certain genetic components of the parents. Although some influence of environmental factors upon age at maturity may exist, it remains to be proven definitely. The more important influences certainly appear to be heritable ones.

These results differ somewhat from those obtained for the Skeena sockeye by Milne (1954), who concluded that although there were indications of both hereditary and environmental influence upon age at maturity, neither effect could be established from his data. In the present case hereditary influence is strongly and positively indicated in the correlation tests, particularly by the marked inequality of Correlations A and C, and B and D (the tests used by Milne). On the other hand, Milne obtained moderate positive values for Correlations C and D, which led him to suggest that there was "some indication of environmental influence upon age at maturity". With the larger series of years used in this paper, and the transformation of weights to numbers of fish, these two correlations are reduced in magnitude and no longer give any indication of an

effect of environment. It should also be noted that the results of the Rivers Inlet tests agree completely with the present Skeena tests.

No attempt is made here to suggest the mechanism by which heritable factors actually govern, or influence, the age of maturing of the progeny. It is assumed that some mechanism exists through the operation of which mature progeny tend to be reproduced in the same proportions of age-classes as existed in the parental stock. Although such a mechanism might involve segregation of age-classes at spawning, this is considered to be unlikely, or at least not usually extensive.

CHANGES IN AVERAGE ANNUAL SIZE

Comparisons between Sexes

For each of the two age-classes, in both fisheries, comparisons are made between male and female sockeye in anual average weights (Fig. 7) and lengths

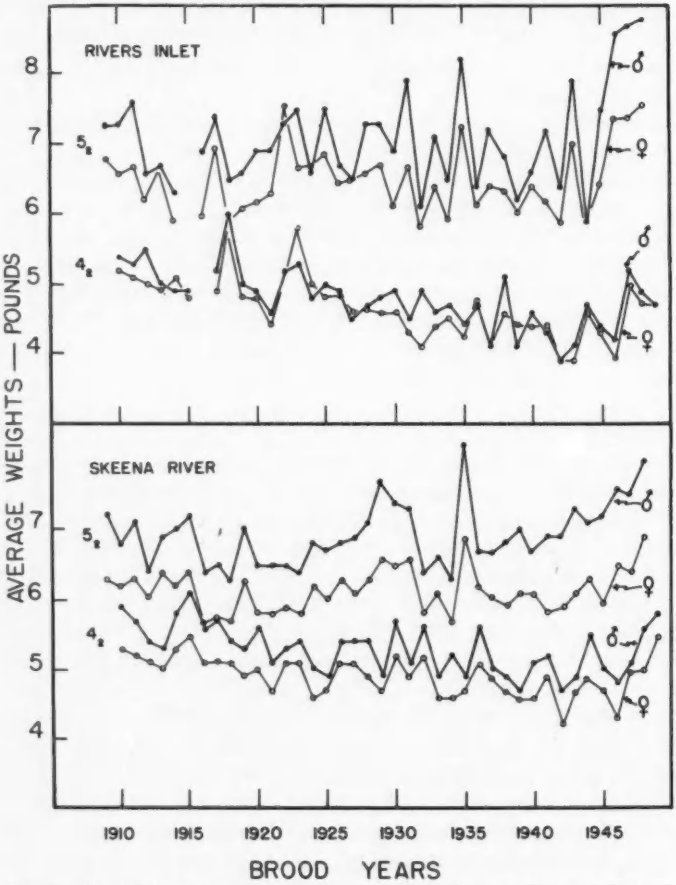

Fig. 7.—Annual average weights of 4_2 and 5_2 sockeye at Rivers Inlet and Skeena River.

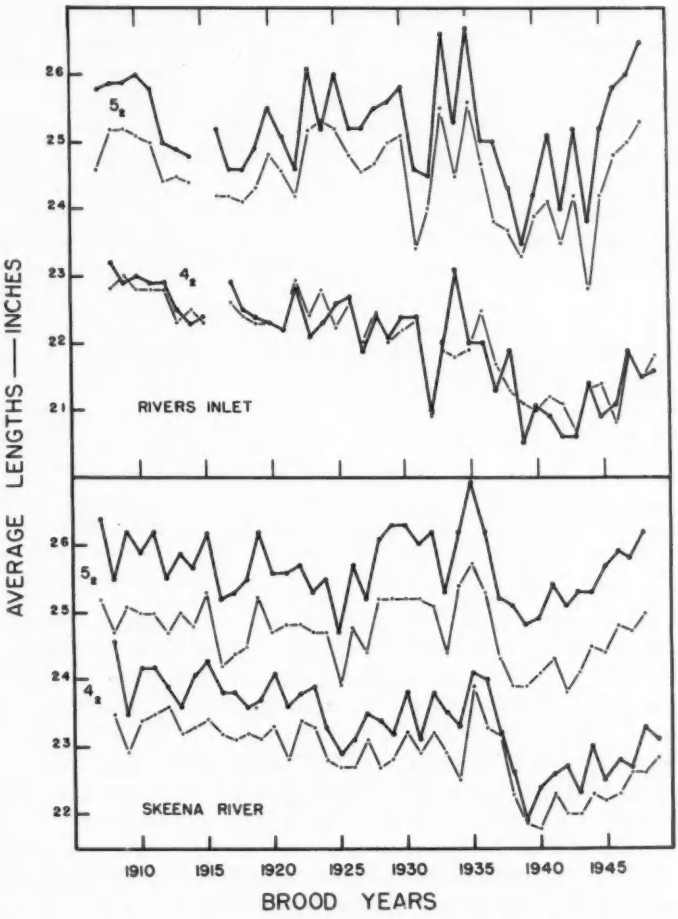

FIG. 8.—Annual average lengths of 4_2 and 5_2 sockeye at Rivers Inlet and Skeena River.

(Fig. 8). These figures show that the two sexes have experienced similar year-to-year variations in annual size as measured by weight and fork length.

COMPARISONS BETWEEN AGE CLASSES

There have been differences between the two age-classes in trends in the year-to-year variations in average size, among both sexes, and in the two fisheries (Fig. 7, 8). The 4_2 fish, of both sexes, experienced a fairly steady decline in average size up to about the brood year 1939, following which there was an average increase in size. The 5_2 fish, on the other hand, of both sexes do not show as distinct a trend, although in the period up to the brood year of 1939 or thereabouts, there appears to have been a slight over-all increase in average size.

The two age-classes have been very similar in their year-to-year changes in average weight and length—that is, they have frequently shown simultaneous increase or decrease in average size in successive years. However, in this respect there has been considerably less similarity between the two age-classes when sizes of fish of the *same brood-year stocks* are compared, than when sizes of fish that were *caught in the same year* are compared. The two kinds of relationship have been tested by the correlation method (Table IV). With each sex, 4_2 and 5_2 fish that were caught in the same year (hence came from different brood-years) were more closely related in respect to their final size than were 4_2 and 5_2 fish that came from the same brood-year stocks (but were caught a year apart).

TABLE IV. Correlations between annual average individual weights of 4_2 and 5_2 sockeye; (a) of fish of the same brood-year stocks; (b) of fish that were caught in the same year. An asterisk denotes a statistically significant relationship.

	Rivers Inlet		Skeena River	
	Males	Females	Males	Females
Between fish of the same brood-year stocks	−0.048	+0.027	−0.179	+0.040
Between fish that were caught in the same year	+0.298	+0.514*	+0.336*	+0.507*

This relationship suggests that variations in the final size of sockeye salmon at the time of maturity are determined mainly by the environmental conditions during the latter part of the ocean phase (the final spring and summer), rather than by the environmental conditions during early freshwater life and/or the early ocean phase. This, in turn, would indicate that the age of maturing in sockeye salmon has already been determined at some early period in its life history, and is not directly dependent upon the growth experienced, and final size attained, during the last of the ocean phase. If this is so then it does not seem likely that maturity in sockeye salmon could be delayed for a year when growth in the current year has been slow (for example, that maturity in normally 4-year-old fish is postponed for a year so that they mature and return as 5-year-old fish).

COMPARISONS BETWEEN RIVER SYSTEMS

Annual average weights of Rivers Inlet and Skeena River sockeye of the two age-classes are compared in Figure 9.

As noted above, the trends of changes in average size, for each sex and each age-class for the brood-year period 1910–1949, were similar at the two rivers.

Year-to-year changes in average weight in the two fisheries have been compared by the correlation method (Table V). The two systems show considerable similarity in such changes for each sex and each age-class; each correlation value listed in Table V being statistically significant at the level $P = .01$. (Comparisons of fork lengths have not been computed.)

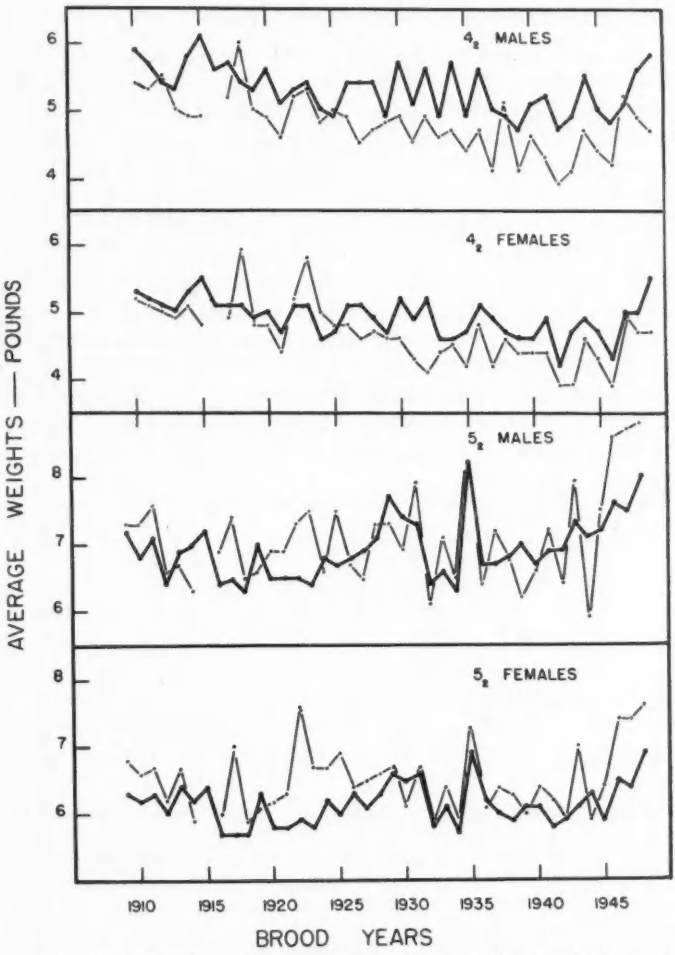

FIG. 9.—Comparisons between Rivers Inlet (thin line) and Skeena River (heavy line) in annual average weights of each sex of 4_2 and 5_2 sockeye.

TABLE V. Correlations between annual average weights of Rivers Inlet and Skeena River sockeye for each sex and each age-class. All values of r shown are statistically significant. (r = correlation coefficient; n = number of variates; P = probability.)

Age-group	Males			Females		
	n	r	P	n	r	P
4_2	39	0.533	<.01	39	0.566	<.01
5_2	39	0.611	<.01	39	0.477	<.01

Changes in Differences in Size between 4_2 and 5_2 Fish

Fish of age 5_2 are longer and heavier on the average than age 4_2 fish, and the annual average weights and fork lengths show these differences. In the two fisheries the difference between the annual average size of 4_2 and 5_2 fish, for each sex, for weight (Fig. 10) and length (Fig. 11), has increased during 1908–1949. This increase appears to have resulted from the decline in the average size of 4_2 fish over a period during which the average size of 5_2 fish remained relatively constant or even showed a slight increase. A complete explanation of this trend does not seem possible at this time, but it might be an effect of fishing with gill nets that are selective for size, these exerting a steady selection pressure against fish of the abundant intermediate sizes. If the nets in use tend to take fish of exactly median size most efficiently, then the average size of 5_2's in the catches should increase over a period of years, and that of 4_2's should decrease. The Rivers Inlet and Skeena River data merely suggest the first effect, but show the second clearly. If, however, there is a preference among fishermen for larger-than-average fish, then the nets being used would tend to fish the upper half of the length distri-

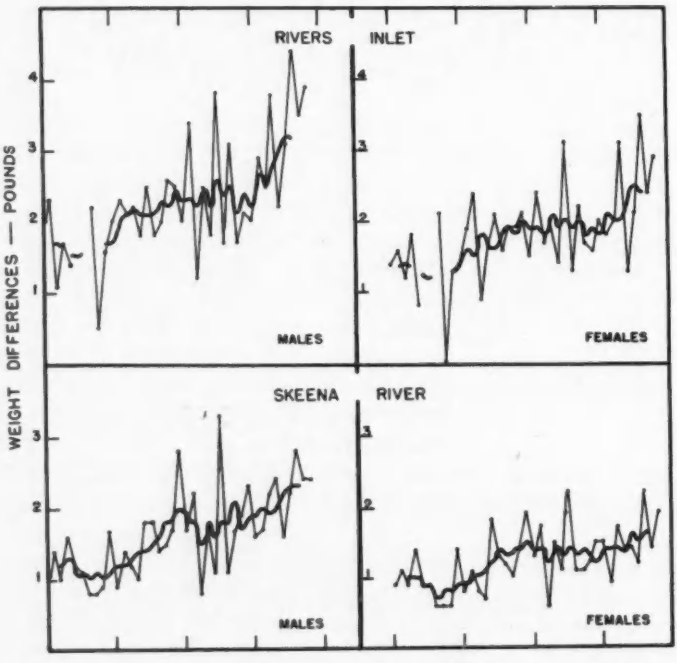

Fig. 10.—Rivers Inlet and Skeena River—annual differences in average weights between 4_2 and 5_2 sockeye of the same brood-year stocks, for each sex. (Heavy line is running average of 5's.)

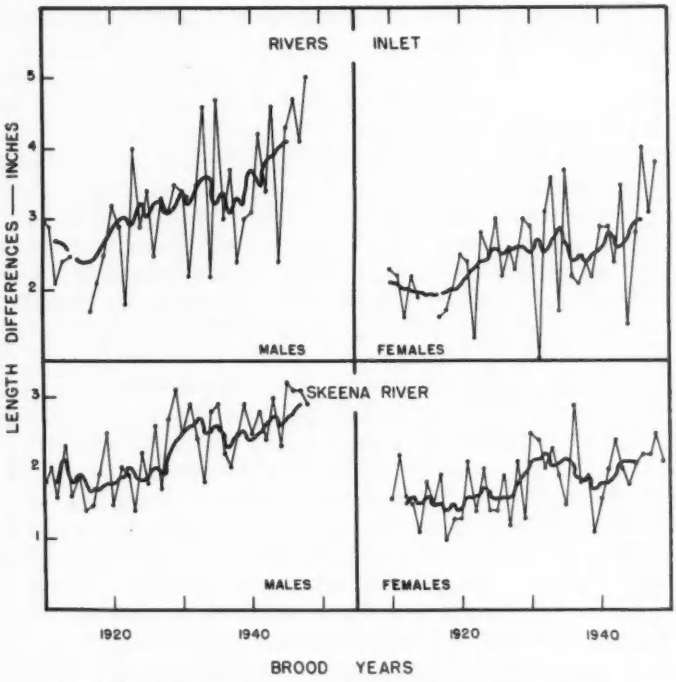

FIG. 11.—Rivers Inlet and Skeena River—annual differences in average lengths between 4_2 and 5_2 sockeye of the same brood-year stocks, for each sex. (Heavy line is running average of 5's.)

bution somewhat harder than the lower half. The effect would be to intensify the selection favouring survival of smaller 4_2 fish, and to weaken (but not eliminate) selection favouring survival of larger 5_2 fish—which would result in the observed situation.

SUMMARY AND CONCLUSIONS

Some characteristics of the annual sockeye catches at Rivers Inlet and Skeena River during the period 1912–1954 have been compared. Discharging into the Pacific Ocean on the British Columbia coast, the two rivers are separated by roughly 200 miles, and have quite different climatological and other physical properties. Because of these differences it was felt that comparisons, between the two rivers, of changes in abundance of different age-classes would help to determine the relative importance of hereditary, as opposed to environmental, influences upon age at maturity in sockeye salmon.

Although several age-classes of sockeye occur in the two populations, 4_2 and 5_2 fish make up the great bulk of the adult returns; therefore, only these two age-groups have been dealt with here.

In several of the analyses it was necessary to make the assumption that the annual sampling to determine the age composition of the catch gave proportions that were significantly representative not only of the catch but of the escapement also. This could not be proven, and to some extent the assumption is known to be incorrect. However, it was felt that any discrepancies were not great enough to detract seriously from the value of such analyses as were attempted.

There was considerable similarity between the two rivers in the sizes of the annual catches and in the manner in which fluctuations in abundance had occurred. A principal difference was a decline in the Skeena catch over the period of 1915–1930 which involved mainly a decline in the catches of 5_2 rather than 4_2 fish. At both rivers the catches of 4_2 fish have been relatively constant; and in each fishery high and low catches of both age-classes have been of similar magnitude.

In the two fisheries there were peak catches separated by 5-year intervals among the 5_2 fish early in the 1912–1954 period; and among the 4_2 fish, there were peak catches separated by 4-year intervals late in the 1912–1954 period. These peak catches did not occur simultaneously in the two systems but were usually a year apart. It was suggested that these cyclic trends in the abundance of different age-groups are of the kind that would occur if heritable factors are of major importance in determining age at maturity in sockeye salmon, since more random fluctuation would be expected of environmental influence.

Changes in the proportions of 4_2 and 5_2 fish produced from the same brood-year stocks were also similar in the two systems. In each there were an early and a late period during which 5_2 fish usually dominated the adult returns, and a central period during which 4_2 fish were usually predominant. During the whole period the average numbers of 4_2 and 5_2 fish caught were fairly equal. (Among the actual samples the two age-classes were almost equally represented, in both fisheries.)

The correlation method was used to attempt to determine whether age at maturity was governed mainly by heritable factors or by environmental influences. Corollaries to three independent hypotheses were tested. There was considerable agreement of results between the two populations, with strong indications from both bodies of data that the principal influences upon age at maturity in sockeye salmon were heritable ones. No effect of the environment upon age at maturity could be positively indicated, but the method used did not permit it to be disproven altogether.

The annual sizes of fish in the catches were compared, and it was found: (a) that the two sexes had been very similar in their annual changes in average weight and length; (b) that in the two fisheries the year-to-year changes in average weight and length, for each sex and age-class, had been very similar; (c) that between the two age-classes there had been very similar annual changes in size, for each sex, when fish that had been *caught in the same year* were compared, but not when fish *that belonged to the same brood-year stocks* (caught a year apart) were compared. This fact was interpreted as indicating that final size at time of maturity had been influenced mainly by environmental conditions

during the latter part of the ocean phase, and that these conditions vary. This, in turn, would suggest that the age of maturing in sockeye is determined at an early stage in the life history.

At both Rivers Inlet and Skeena River, the difference in average size between 4_2 and 5_2 fish has increased during 1912–1954. The change was consistent and fairly progressive, for each sex, and for length and weight. A definite explanation of this trend can not be given at this time, but it is probably due to the selective action of the gill nets, which would tend to favour survival of smaller 4_2 fish and larger 5_2 fish.

Indications that heritable factors were of greater importance than environmental influences in governing the age of maturing in sockeye salmon came from the tests for correlation referred to, and also from the fact that among 4_2 and 5_2 sockeye, both at Rivers Inlet and the Skeena River, fluctuations in abundance have tended to occur in 4- and 5-year cycles, respectively.

If, among sockeye salmon, age at maturity could be advanced or delayed a year, depending upon whether the fish had experienced faster or slower growth as a result of environmental conditions, then it would be expected that among populations that have undergone considerable year-to-year variations in length and weight, there would be accompanying variations in the proportions of 4- and 5-year-old fish produced. This does not appear to be the case with Fraser River sockeye. Among these, there have been considerable year-to-year differences in size, yet 4-year-old fish have always made up the great bulk of the adults (the large up-river populations in particular), and 5-year-old fish have never constituted more than a small fraction of the returns.

At Rivers Inlet and Skeena River the levels of abundance of the 4- and 5-year-old sockeye have tended to be stable; and this would be expected if the hereditary influence upon age at maturity were of principal importance. It is suggested that the fluctuations in abundance that have occurred within each age-class have been due to variations in environmental stresses—and these could be effective at any stage in the life history.

It was noted that Rivers Inlet and Skeena River were frequently out of phase in respect to the timing of corresponding levels of abundance. This, of course, could occur if one population experienced some marked environmental event affecting survival at a time when the other did not. The similarity between Rivers Inlet and Skeena River in respect to their variations in annual average lengths and weights suggests that the two populations have experienced the same or similar ocean conditions (since the latter years in the life cycle appear to exert the greatest influence upon the final size attained). Differences in their freshwater or earliest oceanic environmental experiencs, therefore, have probably been mainly responsible for the cycles being out of phase.

That the two systems have produced similar *numbers* of sockeye salmon is probably only coincidence, and merely reflects the fact that each freshwater environment has imposed limitations upon sockeye production at about the same level of magnitude.

Since the two age-groups of sockeye at Rivers Inlet and Skeena River usually

spawn in the same river and at about the same time, it is difficult to conceive that they are segregated during spawning. No indications of behaviour involving selection for size (and thus age) have been reported, as far as is known, although this possibility has never been studied. Some degree of segregation might occur through a difference between the two age-groups in the timing of their spawning migration, since as has been observed on the Skeena, 5-year-old fish tend to arrive on the spawning grounds over a somewhat earlier average period than do the 4-year fish; but the overlap is considerable. Somehow, it is suggested by the writer, the fertilized eggs receive genes that strongly influence the age at which the resulting adults will mature, in proportions that are similar to the age-class composition of the parent stock.

These analyses are not considered as proof of the influence of hereditary factors upon time of maturing in sockeye salmon, but rather as indicative of its possible importance. The writer hopes that more information on this problem will appear from other sources in the near future; its further elucidation should constitute a useful contribution towards management of the sockeye fisheries.

ACKNOWLEDGMENTS

Mr. D. R. Foskett, until recently on the staff of the Nanaimo Station of the Fisheries Research Board of Canada, has made several references in the past, in annual reports and in his "Contributions to the life history of the sockeye salmon" (published in the Report of the British Columbia Department of Fisheries), to the possible relationship between an hereditary determination of age at maturity in sockeye salmon and the fluctuations in the abundance of 4- and 5-year-old sockeye at Rivers Inlet. The writer is pleased to acknowledge these.

The writer is particularly grateful for the advice and suggestions most generously given by Dr. W. E. Ricker, and to Drs. D. B. DeLury, M.P. Shepard, R. E. Foerster, P. A. Larkin, Ferris Neave and W. A. Clemens for reading the manuscript and offering valuable comments.

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Variation with Fish Length, Sex, Stage of Sexual Maturity, and Season in the Appearance and Volume of the Drumming Muscles of the Swim-Bladder in the Haddock, *Melanogrammus aeglefinus* (L.)[1]

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ABSTRACT

Observations made as early as 1947 and data collected in 1953 to 1954 and 1956 to 1957 indicate that there is considerable variation in the size and appearance of the drumming muscles of the swim-bladder of haddock with fish length, sex, sexual maturity, and season on the Grand Bank and St. Pierre Bank. For haddock of the same length the data indicate that the drumming muscles of mature male haddock are larger than those of immature males and also of immature and mature females of the same length. In addition the data indicate that a periodicity is exhibited in the size of the muscles of the mature male, the muscles being nearly twice as large during the pre-spawning and spawning period in May and June as they are in October and November. This phenomenon does not occur in female haddock, the drumming muscles of which are considerably smaller than those of male fish of the same size and show no variation in size with the season.

It is suggested that the difference in size of the drumming muscles of male and female haddock can serve as a means of determining the sex of haddock landed in the gutted condition by commercial trawlers, at least for the mature fish which make up the bulk of the commercial trawlers' catches. There is some difference between male and female haddock in the colour of drumming muscles, but this seems to be of secondary importance for distinguishing between the sexes.

Male haddock probably use the drumming muscles chiefly to produce low-frequency swim-bladder sounds which serve as rallying calls for female and other male haddock to join in spawning activities.

INTRODUCTION

In many teleost fishes there are external to the swim-bladder muscles themselves special groups of muscles attached to the ventral wall of the swim-bladder. These special muscles, composed of striated muscle fibres, are "drumming" muscles which by their contractions vibrate the swim-bladder wall (Jones and Marshall, 1953).

In the European haddock, *Gadus aeglefinus* L., these drumming muscles have been described by Hagman (1921) as lying at the front end of the swim-bladder and being attached entirely on the swim-bladder wall. These drumming muscles had also been described previously by Delaroche (1809).

The senior author noted in 1947, in the early stages of his work on haddock, that the drumming muscles of the swim-bladder of the mature male haddock were much larger than those of the mature female haddock of similar length, that these organs were larger in mature than in immature males of the same length, and that these drumming muscles were particularly large in the males during the spawning season.

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In the pressure of other work further and more detailed observations and measurements of these muscles were delayed until January, 1953, when some measurements of the volume of drumming muscles in relation to length, weight, sex and stage of maturity of the haddock were begun with B. G. H. Johnson. These preliminary investigations continued until April, 1954. The work was begun again with methods slightly changed in co-operation with the junior author. This second and main series of observations was taken between May, 1956, and September, 1957. All data with the exception of those shown in Figure 7 are from this second period.

MATERIAL AND METHODS

For the 1953 and 1954 measurements the thin ventral peritoneal covering of the drumming muscles was removed, the muscles scraped away from the swim-bladder wall and the volume of the drumming muscles measured. This was found to be much too slow, so in 1956 and 1957 the individual drumming muscles were cut out of the swim-bladder and the projecting portions of the swim-bladder wall removed (Fig. 3B).* Total volumes, in each case including both drumming muscles, were measured in a 10 cc. cylinder graduated to 0.2 cc. and were read to 0.1 cc.

A test was carried out in order to decide whether there was any likelihood that significant differences between swim-bladder volumes could possibly be due to the amount of swim-bladder and peritoneal tissue left attached to the actual drumming muscles in the second set of experiments. The drumming muscles from 9 mature male and 2 mature female haddock, 44 to 63 cm. in length, taken from St. Pierre Bank on Oct. 17, 1956, consisted of 93.2% drumming muscle tissue, by volume, and 6.8% attached swim-bladder and peritoneal tissue. Since this test was made at a season when the drumming muscles of the mature males had decreased in size, the 6.8% can be considered to be close to the maximum amount of material other than actual muscle to be included in the drumming muscle volumes at any time during the year. Doubtless at spawning time the actual muscle tissue in the males would be an even higher percentage of the total volume. The seasonal changes in the drumming muscles to be described in this paper are of such great magnitude that they must be due mainly to changes in actual muscle bulk and not to changes in the attached swim-bladder and peritoneal coverings.

The stage of maturity was usually checked by the senior author and, in his occasional absence, by T. K. Pitt and the junior author. In this paper all fish which are maturing toward spawning or show signs of having spawned are included in the mature category, the remainder being called immature.

Haddock lengths, snout to the end of the mid-fork of the caudal fin, were measured to the nearest centimetre on a measuring board with the first space 1½ cm. long, and thus succeeding centimetre lengths fell in the middle of the centimetre space.

The photographs of haddock drumming muscles in this paper were taken by E. L. Rowe.

*Figures 1–6 on insert following page 370.

OBSERVATIONS ON THE DRUMMING MUSCLES OF MALE AND FEMALE HADDOCK

Description and Location

Near the anterior end of the haddock swim-bladder and closely applied to its ventral wall is a pair of elongate muscular structures, rounded at the posterior end but slightly pointed anteriorly. The muscle masses lie entirely on the swim-bladder wall in the shape of a V with the open part of the V pointing posteriorly. Anteriorly for about one-half of the distance along the medial edges the muscles lie close together. Their length occupies approximately one-quarter of the length of the swim-bladder. Figure 1A is a photograph of the drumming muscles of a mature male haddock *in situ* with the thin black peritoneum, which lines the body cavity and also covers the drumming muscles, stripped away except from the drumming muscles themselves. In Figure 1B the peritoneum has been left intact.

The fibres of the drumming muscle are of the striated type as seen in cross section (Fig. 2C), and run almost at right angles to its length—slightly obliquely from the medial edge anteriorly to the lateral edge. Laterally the muscle is attached over its entire length to the margin of the swim-bladder wall, and medially the attachment occurs close to the mid-line (Fig. 2A, B). Actually the muscle is embedded in a pocket of the ventral wall of the swim-bladder, the edge of the pocket extending somewhat ventrally around the muscle. This is clearly shown in Figure 3A and diagrammatically in Figure 3B. The whitish edge of the swim-bladder pocket can be seen extending ventrally around the medial-ventral part of the drumming muscles for the male in Figure IB and for both the male and female of Figure 6. The portion of the ventral wall within the pocket is much thinner than it is elsewhere.

Difference in Size and Colour of Drumming Muscles in Male and Female Haddock

In Figure 4 are shown the relative sizes of the drumming muscles of male and female haddock of approximately the same length, taken in May, 1957.

It will be noted that the drumming muscles of male haddock are considerably larger than those of females of the same length, the volumes of the former being 6 to 9 times those of the latter for the three pairs shown. For the male in Figure 4F the handling prior to photographing resulted in the peritoneum becoming rolled up uncovering the muscle tissue on the left side of the muscle. The drumming muscle of the female is very flat on the swim-bladder wall, usually no more than 2 or 3 mm. in thickness, whereas that of the mature male is much thicker. Evidence of the relative thickness of the drumming muscles of the male and female, for fish of the same size, is shown in Figure 5. Both male and female haddock are mature and 52 cm. in length, but the volume of the two drumming muscles is 7.1 cc. for the male as compared with 1.5 cc. for the female. In both cases the peritoneum has been stripped from the body wall but left covering the muscles for contrast.

For mature haddock there appears to be some slight difference in the colour

of the male and female drumming muscles as viewed *in situ*, particularly in the larger haddock. When viewed with the peritoneum intact the colour of the muscles of the male ranges from black in the smaller haddock to reddish brown in the larger fish over 50 cm. in length, while for female haddock the colour of the muscles ranges from black in the smaller to a brownish grey in the larger fish. Exceptions may occur, however, for the drumming muscles of some large haddock of both sexes may appear almost black.

When the thin pigmented peritoneum is stripped off, the drumming muscles of the mature male for all sizes of fish tend to be reddish flesh-coloured, while on the average the muscles of the female appear to be a somewhat lighter or greyish colour without the tint of red. In both males and females there is a considerable range in the amount of black pigment in the peritoneum covering the drumming muscles. In the smaller fish the peritoneum tends to be black or almost black, and there is a decrease in the amount of black pigment with increase in size of fish. In these and other haddock with heavily pigmented peritoneum the actual colour of the muscle tissue of both male and female haddock does not show through the peritoneum. If, however, the peritoneum is only slightly pigmented as occurs more generally in the larger fish, the colour of the muscle tissue does show through, and the drumming muscles of the male appear to be darker than those of the female when viewed with the peritoneum intact. This probably often accounts for the greater part of the difference in the colour of the drumming muscles of the larger male and female haddock without the peritoneum removed. Figure 6 shows the drumming muscles *in situ* of both a male and a female haddock of 49 and 51 cm. in length respectively, with the pigmented peritoneum stripped off. This is an extreme case. Evidence of the slightly darker appearance of the males can also be seen in Figures 4 and 5.

RELATION OF ACTUAL VOLUME OF THE DRUMMING MUSCLES OF THE SWIM-BLADDER TO THE LENGTH, SEX AND SEXUAL MATURITY OF THE HADDOCK AND TO THE SEASON

Figure 7 shows records of the volume of the drumming muscles of individual haddock obtained January, 1953 to April, 1954. These preliminary observations showed well the differences between the drumming muscle volumes of mature males and mature females, and the similarity of the drumming muscle volumes in immature and mature females. It is also indicated that the volumes of the drumming muscles of mature males in June is greater than in January–February.

Mature Males and Season

Tables I to V, at the end of the paper, show for the Grand Bank and St. Pierre Bank the relation between the average total volume of the two drumming muscles of the haddock swim-bladder, and the length, sex, stage of sexual maturity, season and weight of the fish.

The volume of the drumming muscles of mature male haddock, and the ratio of drumming muscle volume to fish weight, (hereafter called the V:W ratio), are greater in May–June than in January, March–April, August–September or

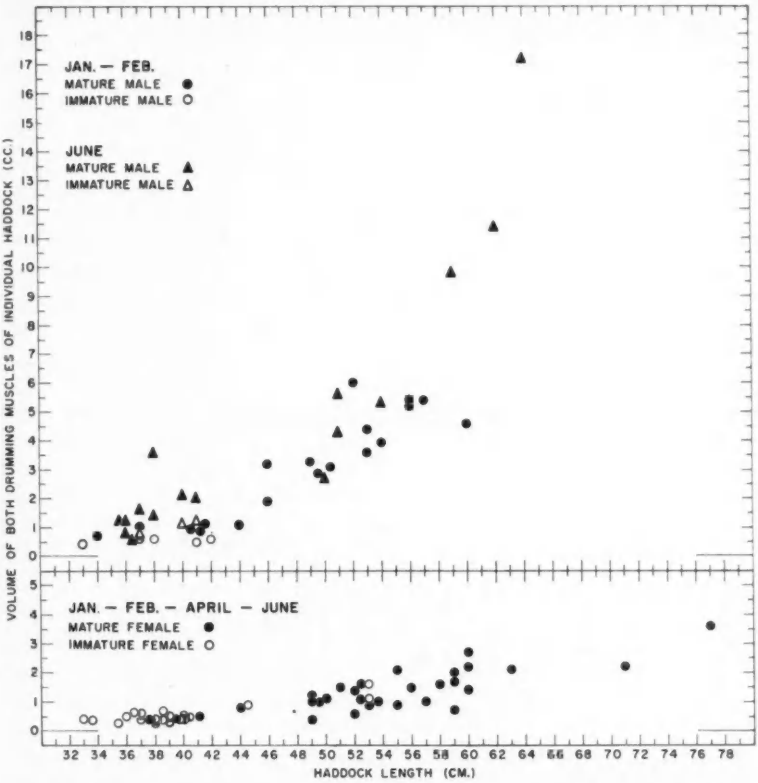

FIG. 7. Volumes of both drumming muscles of the swim-bladder of individual haddock from the Grand Bank, 1953 to 1954.

October–November (Tables I, III, IV; Fig. 8, 9). In Figures 8 and 9 the differences for St. Pierre Bank in the June and October periods are very great.

Judging from the females, these haddock populations on the Grand Bank and St. Pierre Bank spawned in 1956 and 1957 mainly in June and early July, with a very little spawning in May, and probably some in later July. Almost all the males, however, were ripe, with milt in the vasa deferentia, in May, and usually in June they were recorded as partly spent. The drumming muscles of the mature male haddock are also largest at this May–June period; by August–September they are reduced to close to their smallest size, which in the periods under observation occurred in October–November. In January on the Grand Bank the volume of the drumming muscles is close to that of November but slightly higher. By March–April they are increasing toward the enlarged condition which exists at spawning time, but in some cases these muscles must still grow considerably before reaching their maximum size a month or two later.

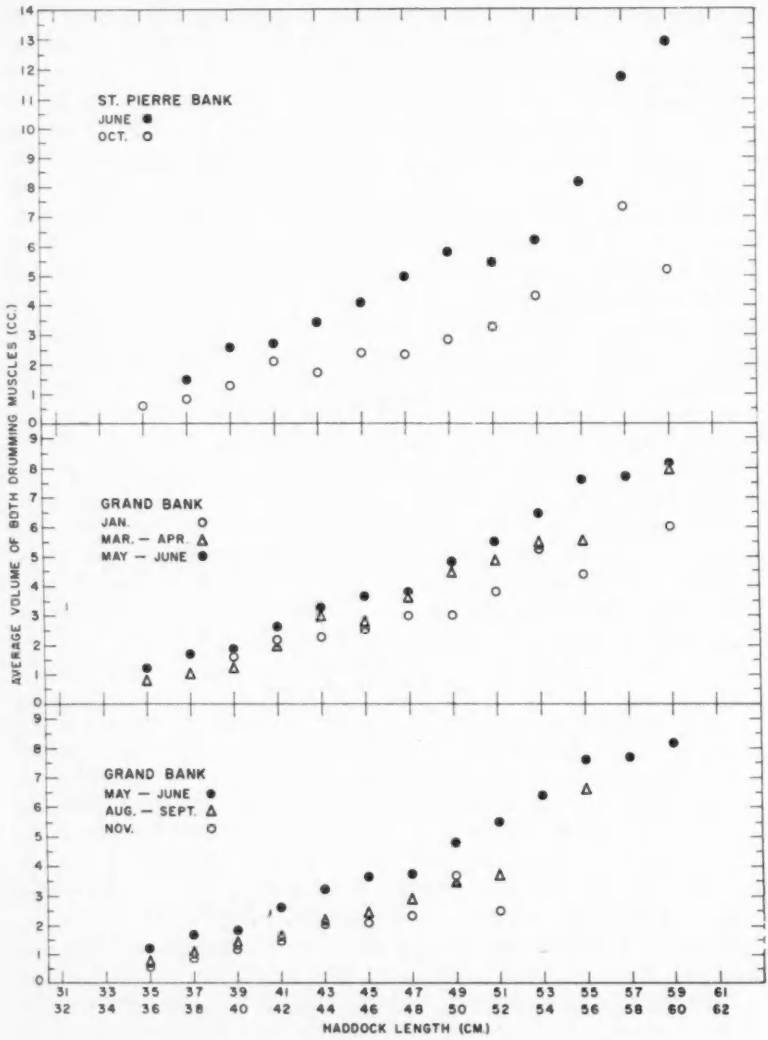

FIG. 8. Average volumes of both drumming muscles of the swim-bladder of mature male haddock from the Grand Bank and from St. Pierre Bank, 1956 to 1957.

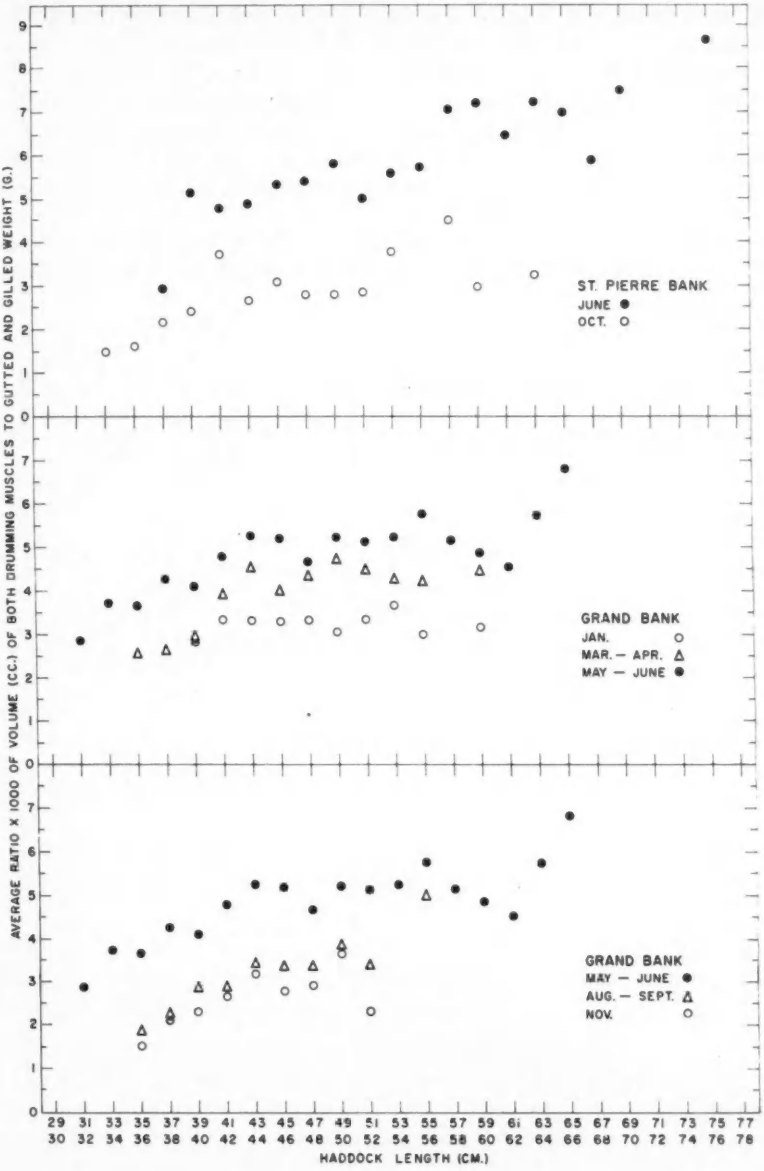

FIG. 9. Average ratios (× 1000) of the volume of both drumming muscles to the gutted and gilled weight of mature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

The V:W ratio in the mature males increases for St. Pierre Bank in June with increase in size of fish. For the Grand Bank at all periods there is an initial increase and a levelling off (Fig. 9; Tables I, III, and IV). The upper points in these curves represent very few fish and the explanation of the difference in trend between St. Pierre Bank and Grand Bank at the larger sizes may lie in the relation of the size of the drumming muscles to the age of the fish, particularly to the number of spawning years. Further research will be needed to provide a complete explanation of this difference.

Figure 10 shows the volumes, and Figure 11 the V:W ratios, of paired drumming muscles from individual mature male haddock for May–June and for

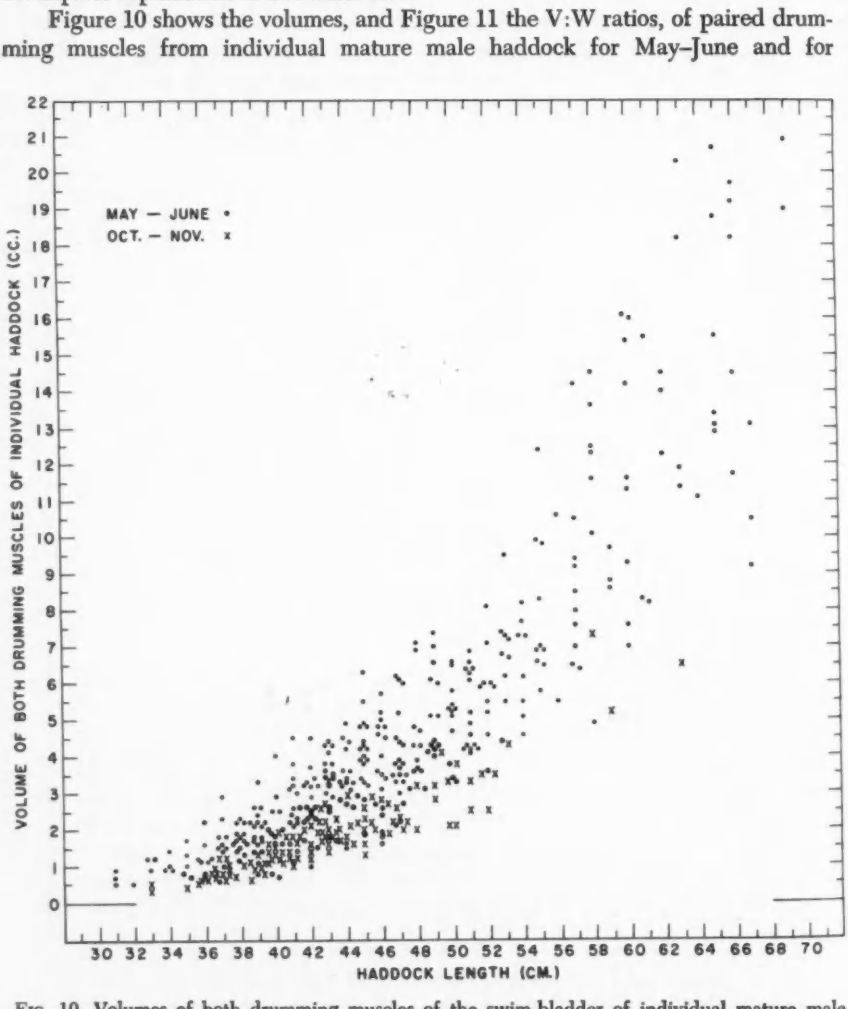

FIG. 10. Volumes of both drumming muscles of the swim-bladder of individual mature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957. (Two values, 25 cc. at 67 cm. and 31 cc. at 76 cm. have been omitted in this figure.)

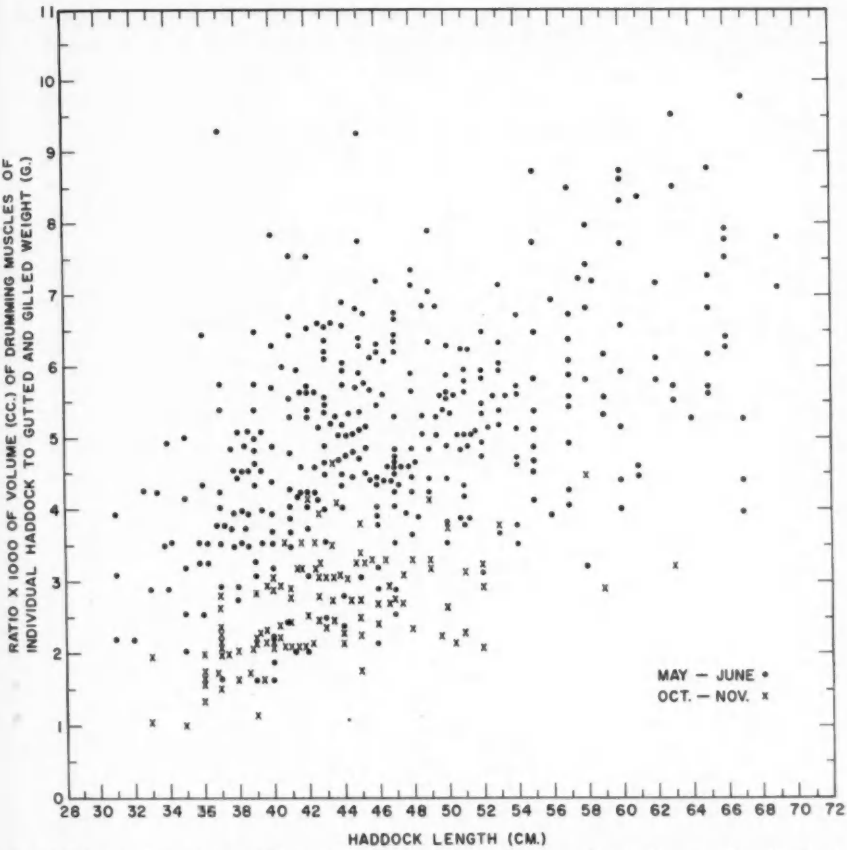
RATIO X 1000 OF VOLUME (CC.) OF DRUMMING MUSCLES OF INDIVIDUAL HADDOCK TO GUTTED AND GILLED WEIGHT (G.)
HADDOCK LENGTH (CM.)
MAY — JUNE •
OCT. — NOV. x

FIG. 11. Ratios ($\times$ 1000) of the volume of both drumming muscles to the gutted and gilled weight of individual mature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

October–November. In both the actual volumes and the ratios there is, for haddock of the same length, an overlapping between the lower ranges of values for May–June and the values for October–November.

MATURE FEMALES, IMMATURE MALES AND FEMALES AND SEASON

Table I to V and Figures 21 and 22 indicate that there is little or no difference in the volumes of the drumming muscles of mature female, immature male and immature female haddock, at the May–June pre-spawning and spawning season and at other periods of the year.

MATURE MALES AND MATURE FEMALES

At all seasons and at all sizes there is a wide difference in the average volume of the drumming muscles, and in the V:W ratio, among mature male

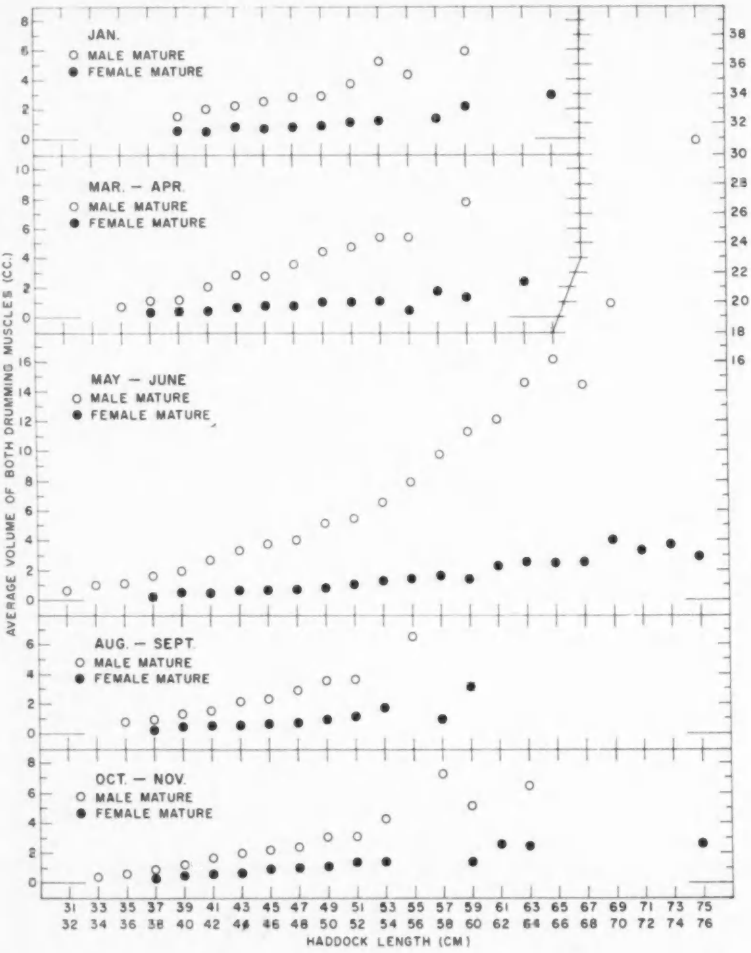

FIG. 12. Average volumes of both drumming muscles of the swim-bladder of mature male and mature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

and mature female haddock (Tables I–V; Fig. 12, 13). For the mature females the ratio increases only slightly, if at all, with increase in fish length. For mature males there is an initial rapid increase in the ratio with either a continued increase or a levelling off at the larger sizes (see earlier discussion with regard to Fig. 8).

Both in May–June and in October–November, the volume of the drumming

muscles and the V:W ratio of individual mature male haddock are distinctly separated from those of mature female haddock, except for a few individuals at the smaller sizes (Fig. 14, 15).

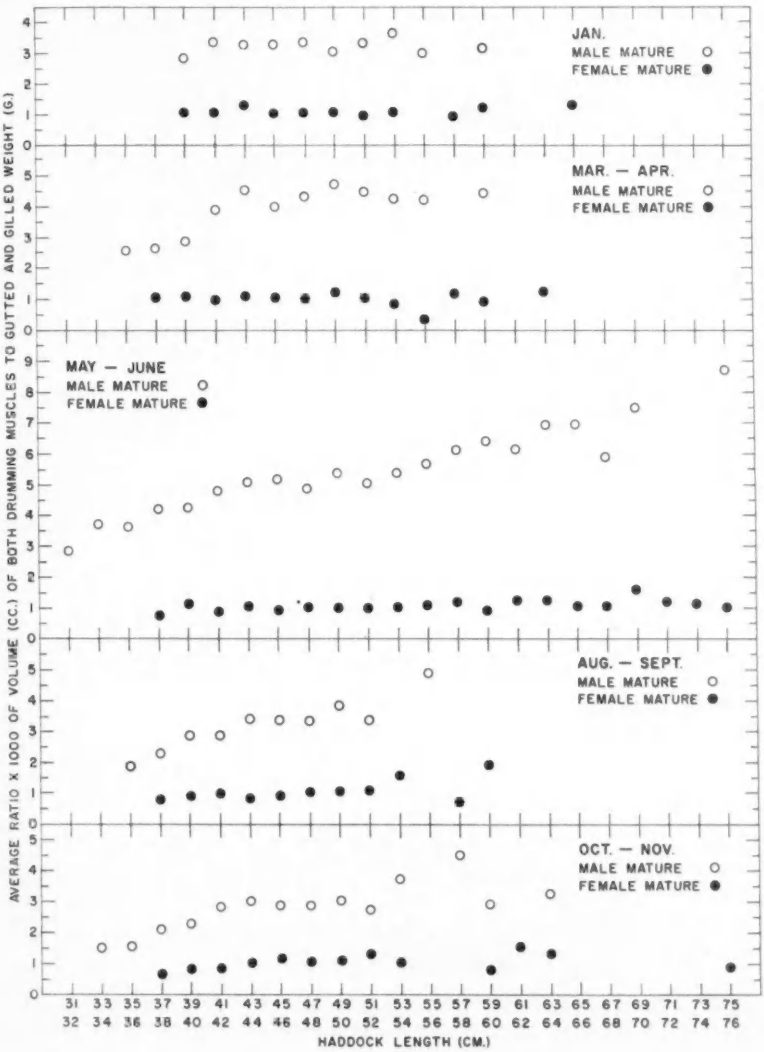

FIG. 13. Average ratios (× 1000) of the volume of both drumming muscles to the gutted and gilled weight of mature male and mature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

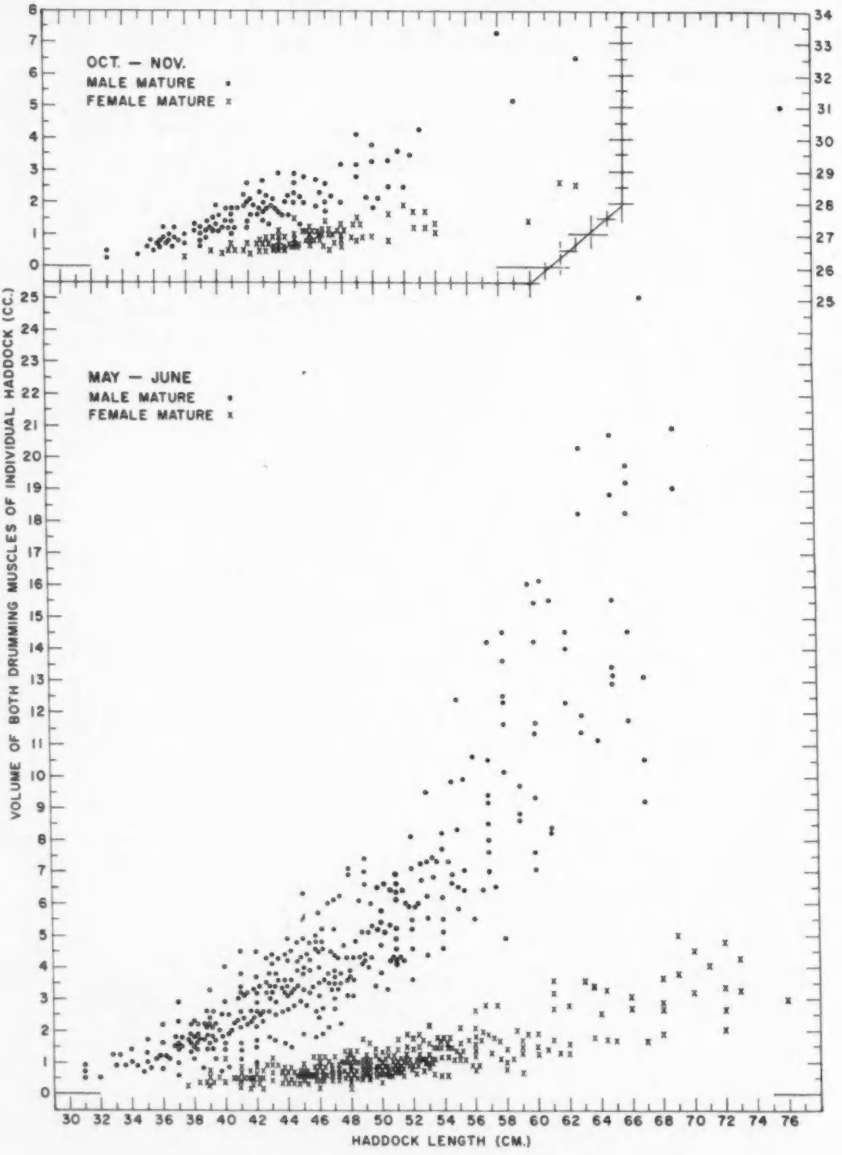

FIG. 14. Volumes of both drumming muscles of the swim-bladder of individual mature male and mature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

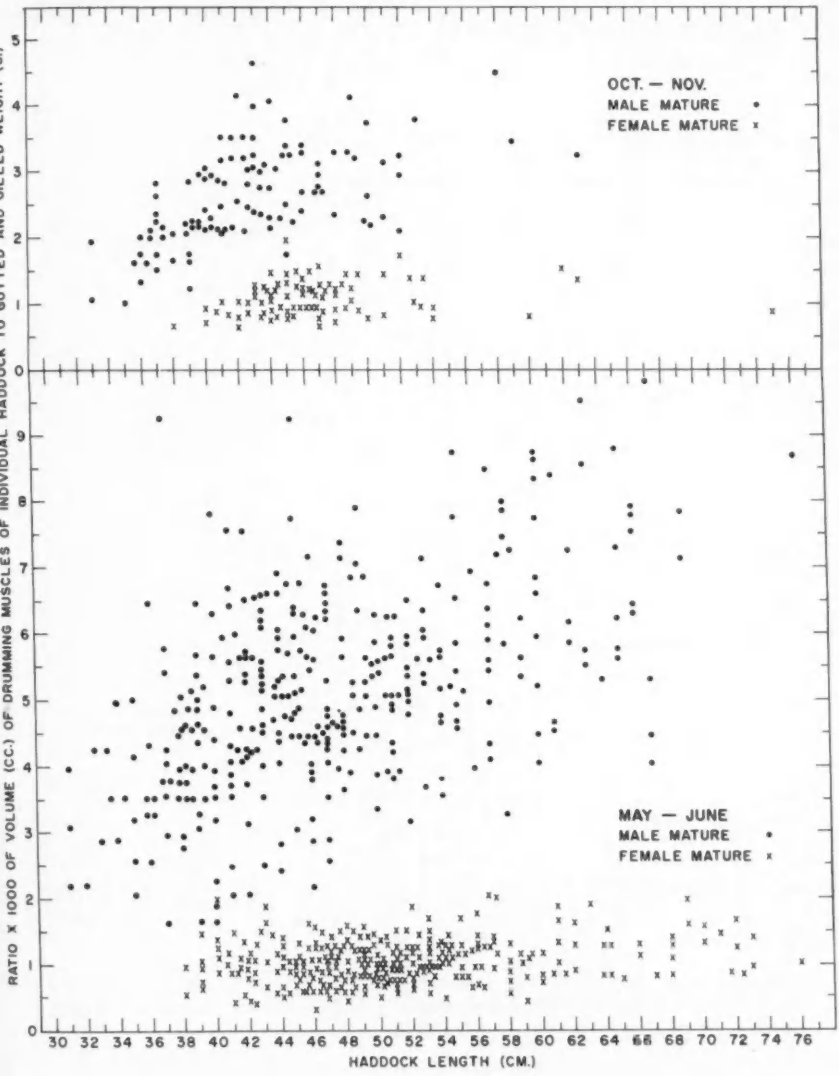
OCT. — NOV.
MALE MATURE
FEMALE MATURE
MAY — JUNE
MALE MATURE
FEMALE MATURE
RATIO X 1000 OF VOLUME (CC.) OF DRUMMING MUSCLES OF INDIVIDUAL HADDOCK TO GUTTED AND GILLED WEIGHT (G.)
HADDOCK LENGTH (CM.)

FIG. 15. Ratios ($\times$ 1000) of the volume of both drumming muscles to the gutted and gilled weight of individual mature male and mature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

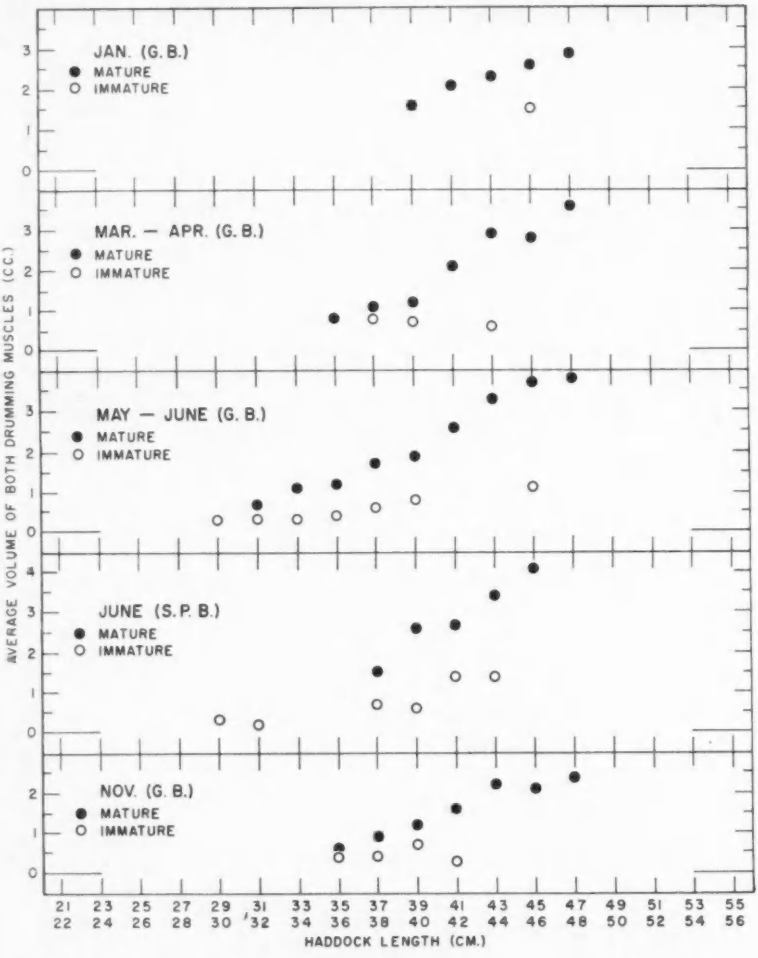

FIG. 16. Average volumes of both drumming muscles of the swim-bladder of mature and of immature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

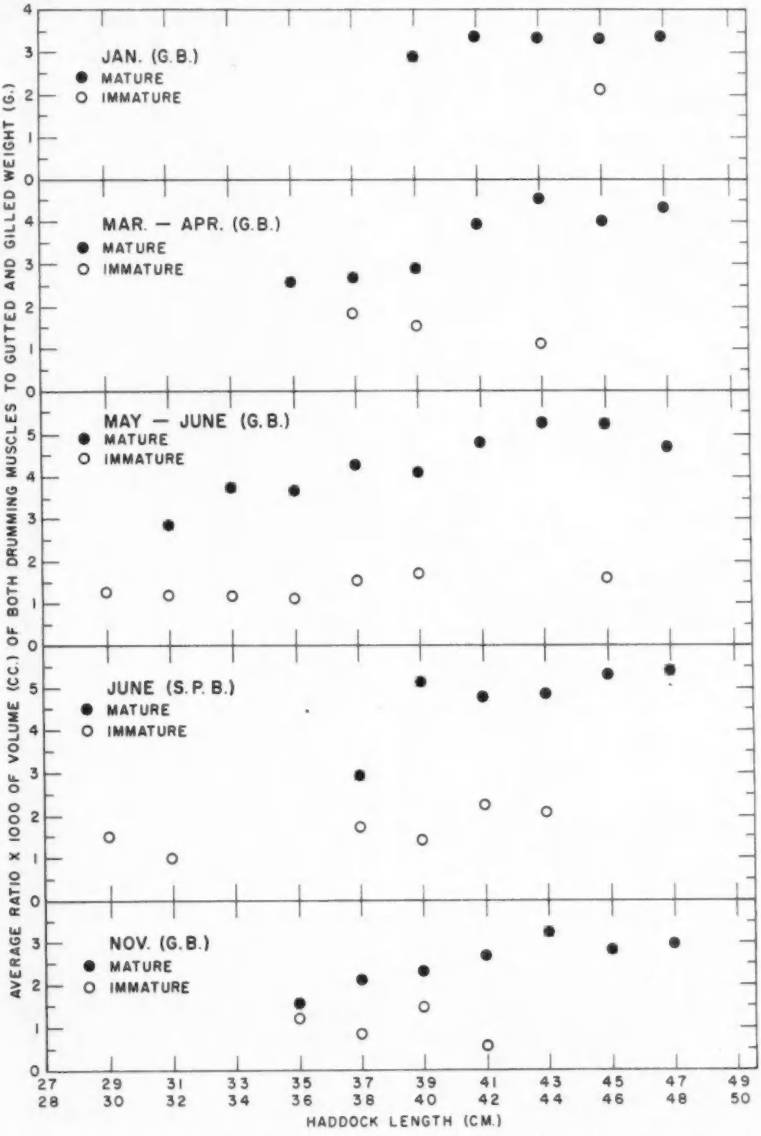

FIG. 17. Average ratios (× 1000) of the volume of both drumming muscles to the gutted and gilled weight of mature and immature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

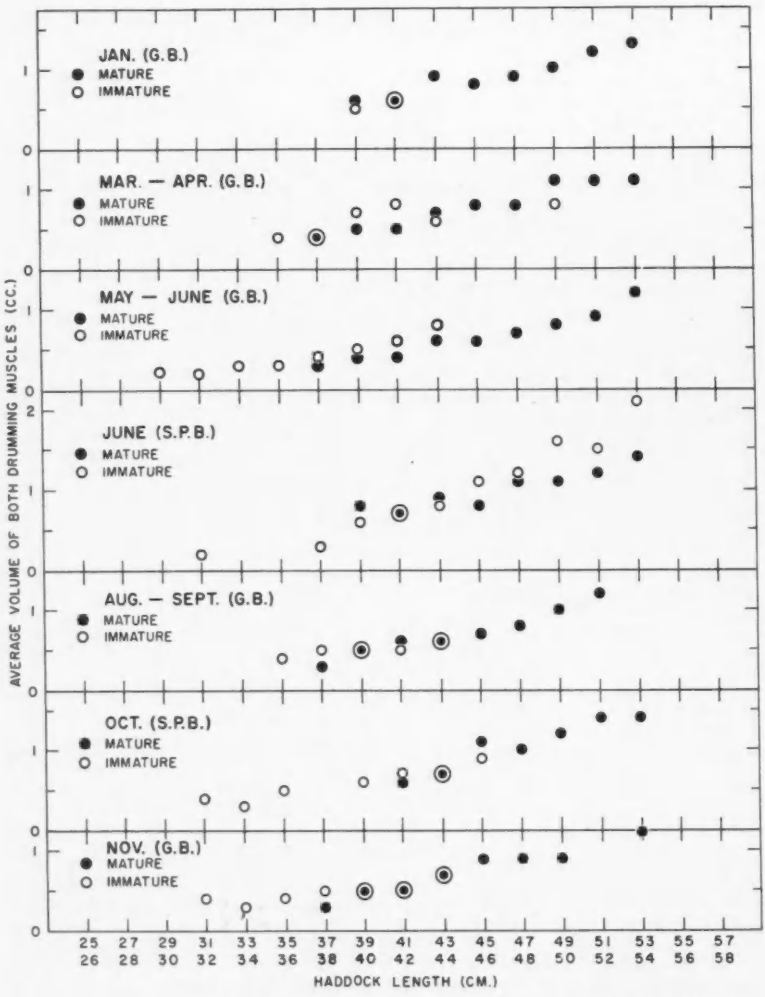

FIG. 18. Average volumes of both drumming muscles of the swim-bladder of mature and immature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

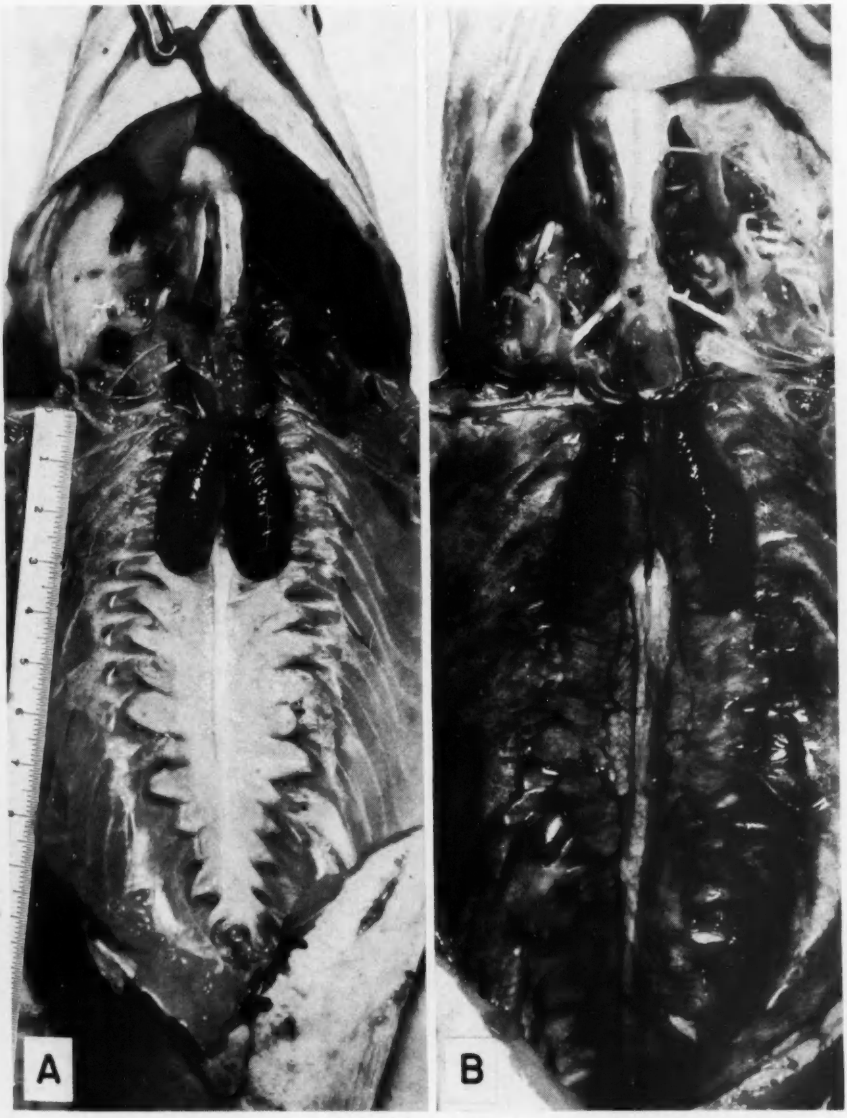

FIG. 1. Ventral view of the swim-bladder (0.75×) showing the drumming muscles of mature male haddock from the Grand Bank, June 15, 1957. A, 44-cm. fish with peritoneum stripped from all but the pair of drumming muscles. B, 61-cm. fish with peritoneum left in place lining the body cavity and covering the drumming muscles.

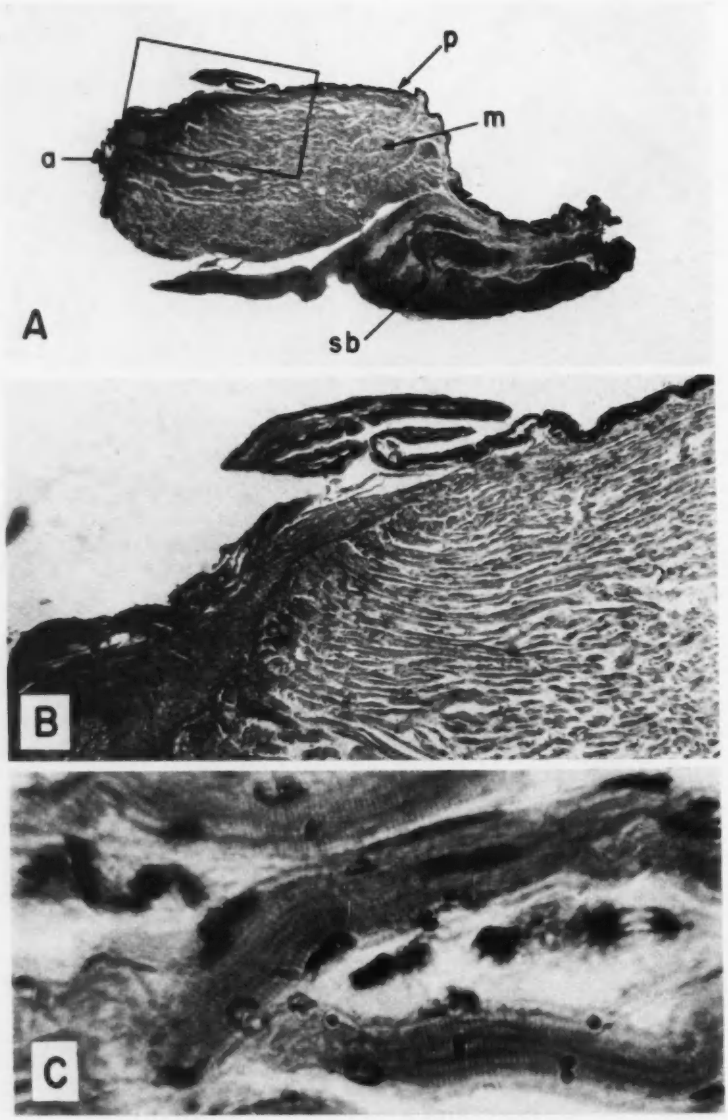

FIG. 2. A, transverse section of a drumming muscle (20×) from the swim-bladder wall of an immature female haddock, 33 cm. in length; a, lateral edge of swim-bladder wall; m, drumming muscle; p, peritoneum; sb, medial thickening of ventral swim-bladder wall. B, magnified portion of a section adjacent to A showing the attachment of drumming muscle fibres to the lateral margin of the swim-bladder wall (80×). C, highly magnified fibres of the drumming muscle showing the striations (1500×).

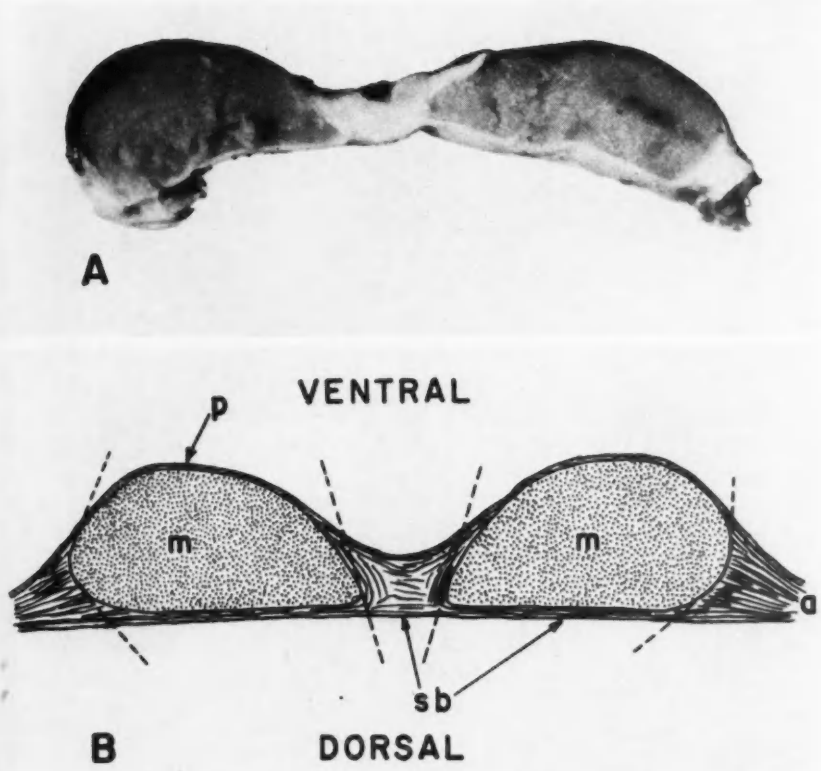

FIG. 3. A, transverse section (3×) of the ventral swim-bladder wall through both drumming muscles of a male haddock from the Grand Bank, Nov. 15, 1957. B, diagrammatic representation of A; a, swim-bladder wall attachment to body wall; m, drumming muscles; p, peritoneum; sb, ventral swim-bladder wall; broken lines represent approximately where the muscles were cut out of the swim-bladder wall for volume measurements.

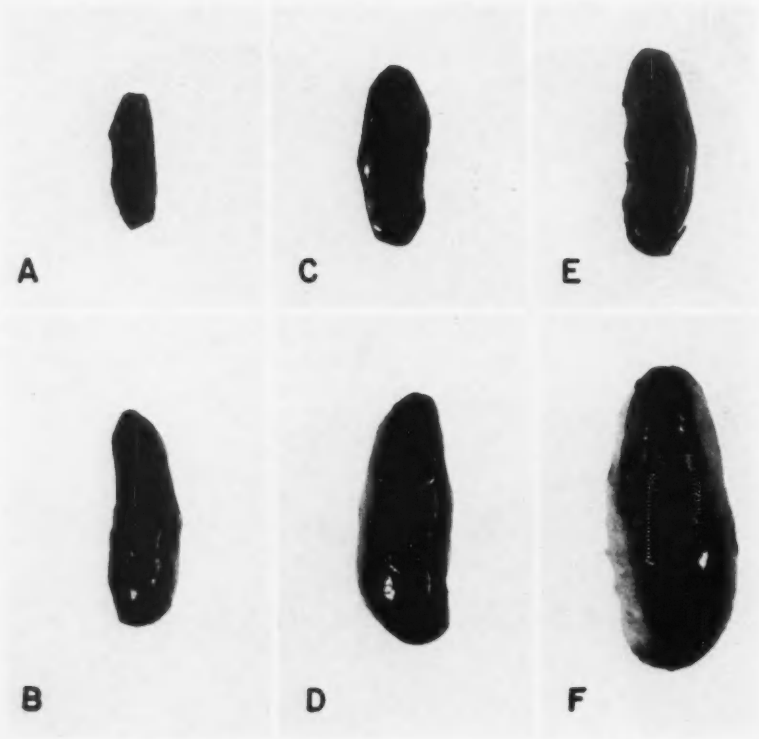

FIG. 4. Ventral view of drumming muscles (1×) from haddock of different sex and size from the Grand Bank, May 24, 1957:

Individual	*Sex and stage of sexual-maturity*	*Fish length*	*Vol. one drumming muscle*
		cm.	*cc.*
A	female immature	39	0.2
B	male mature	39	1.1
C	female mature	51	0.3
D	male mature	51	2.1
E	female mature	56	0.5
F	male mature	59	4.3

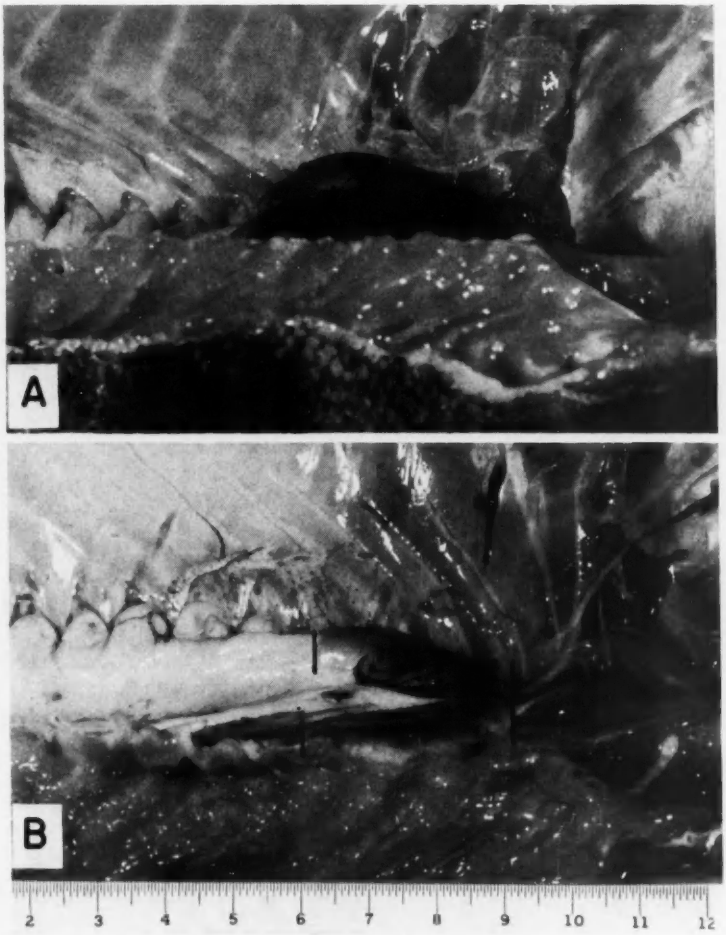

FIG. 5. Drumming muscles of mature haddock from St. Pierre Bank, June 30, 1957, photographed somewhat from the side, with the peritoneum stripped from all but the muscles (1×). A, male; B, female. (The extent of the drumming muscles in B is indicated by black lines.)

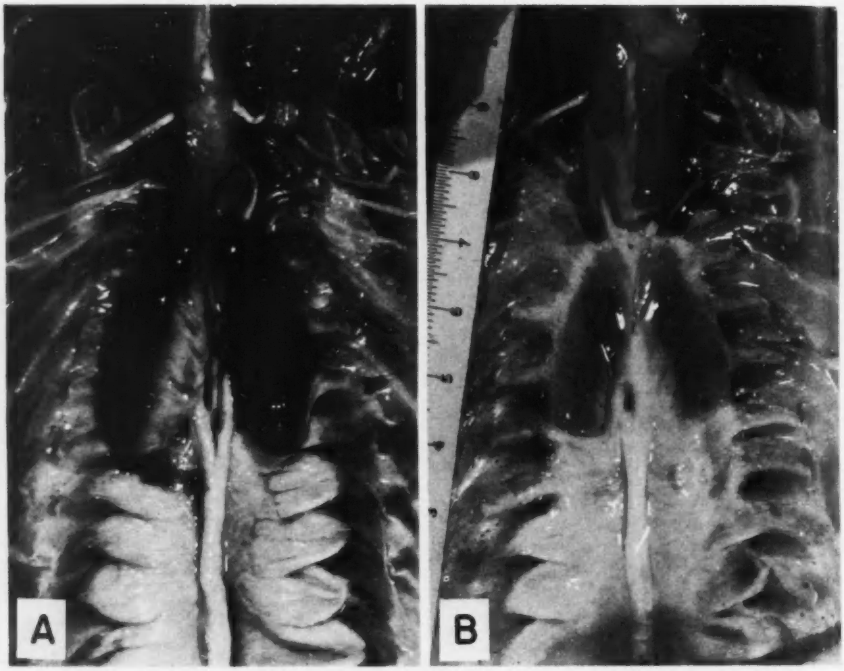

FIG. 6. Ventral view of the drumming muscles (1×) of A, mature male, and B, mature female haddock from St. Pierre Bank, June 30, 1957, with the peritoneum stripped from the body cavity and the muscles.

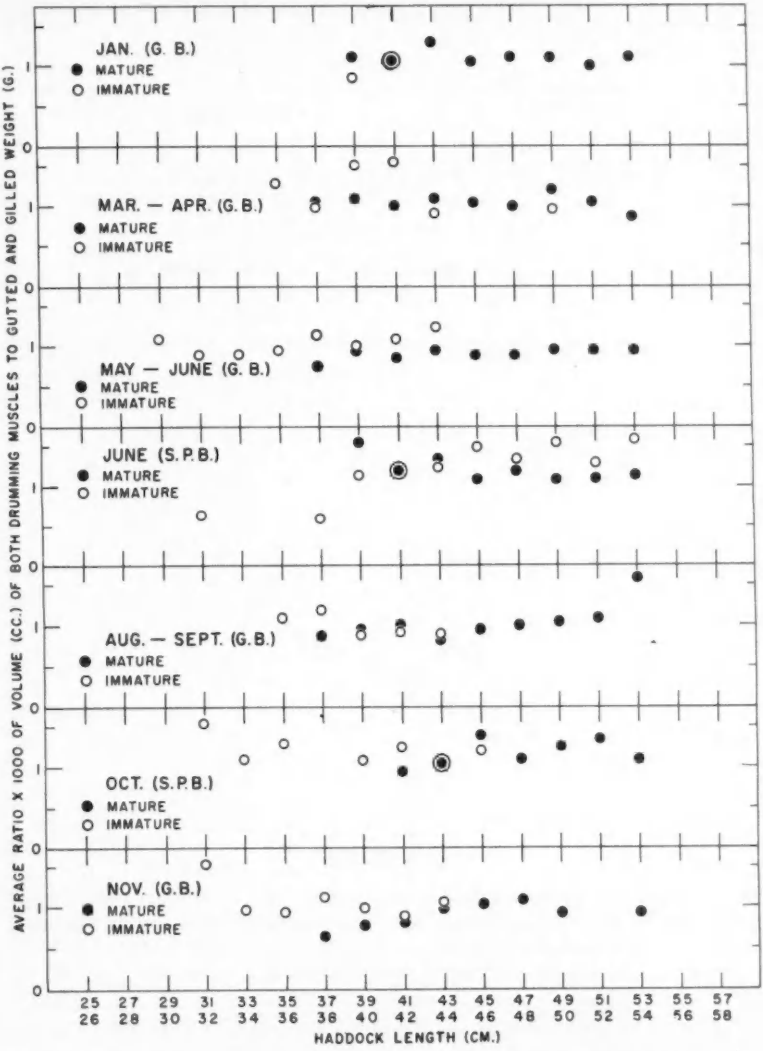

FIG. 19. Average ratios ($\times$ 1000) of the volume of both drumming muscles to the gutted and gilled weight of mature and immature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957.

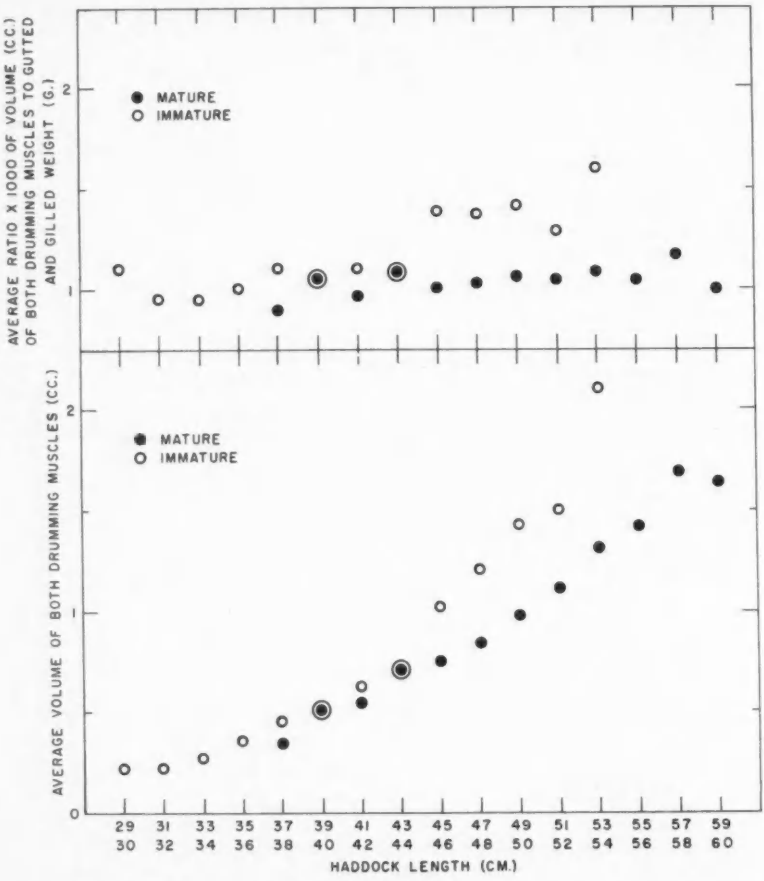
AVERAGE RATIO X 1000 OF VOLUME (C.C.) OF BOTH DRUMMING MUSCLES TO GUTTED AND GILLED WEIGHT (G.)
MATURE
IMMATURE
AVERAGE VOLUME OF BOTH DRUMMING MUSCLES (C.C.)
MATURE
IMMATURE
0
1
2
29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60
HADDOCK LENGTH (CM.)

FIG. 20. Average volumes (both actual and relative to the gutted and gilled weight of the fish) of both drumming muscles of the swim-bladder of mature and of immature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957. (All data for all months are included.)

IMMATURE AND MATURE MALES AND IMMATURE AND MATURE FEMALES

The average volume of the drumming muscles and the V:W ratio for mature males are distinctly greater than those for immature males at all sizes and at all seasons (Fig 16, 17; Tables I, III, V). The differences increase with increase in fish length.

There does not appear to be any considerable or consistent difference between the average volumes of the drumming muscles in immature male and immature and mature female haddock of the same length (Fig. 18, 19; Tables

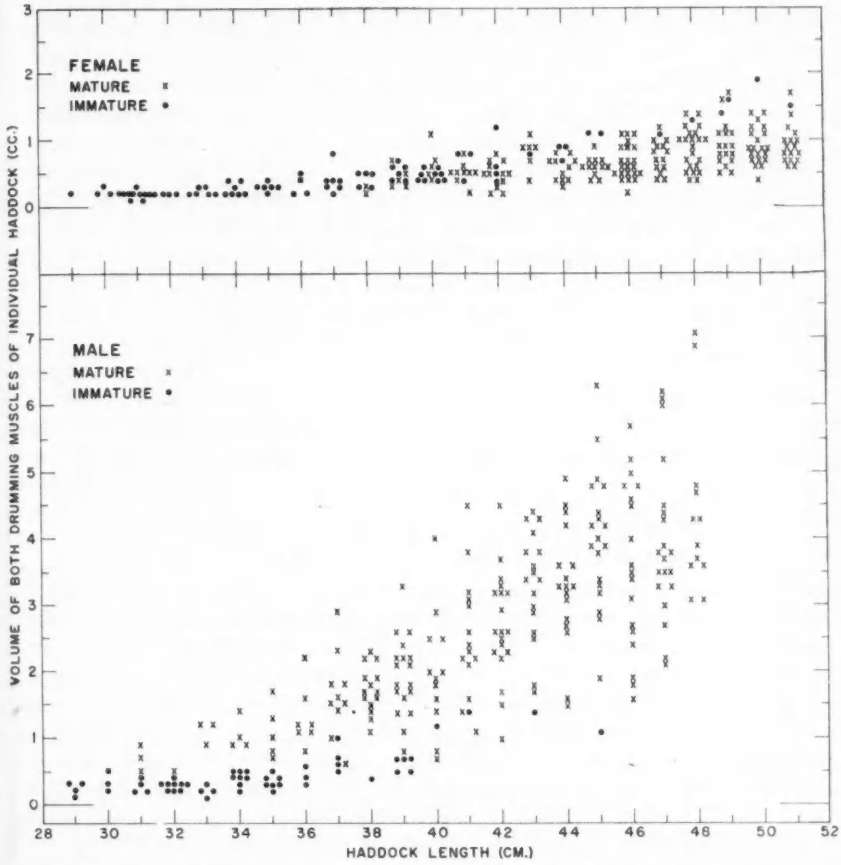

FIG. 21. Volumes of both drumming muscles of individual mature and immature male and female haddock from the Grand Bank and St. Pierre Bank, May–June, 1956 and 1957.

II, III, V). An exception may be the larger immature females of St. Pierre Bank and possibly also of the Grand Bank in the May–June pre-spawning and spawning period. Since there does not appear to be in these data any consistent or significant difference between the volumes of the drumming muscles of female haddock at different seasons, in Figure 20 and Table VI all the data for mature and immature females have been combined for all seasons of the year. Both in the combined data and in the seasonal data there is a tendency for the volume of the drumming muscles to be greater in *immature* than in mature female haddock, especially at the larger sizes. It seems possible that females which have delayed maturity may have something of a male character which causes the gland to enlarge slightly

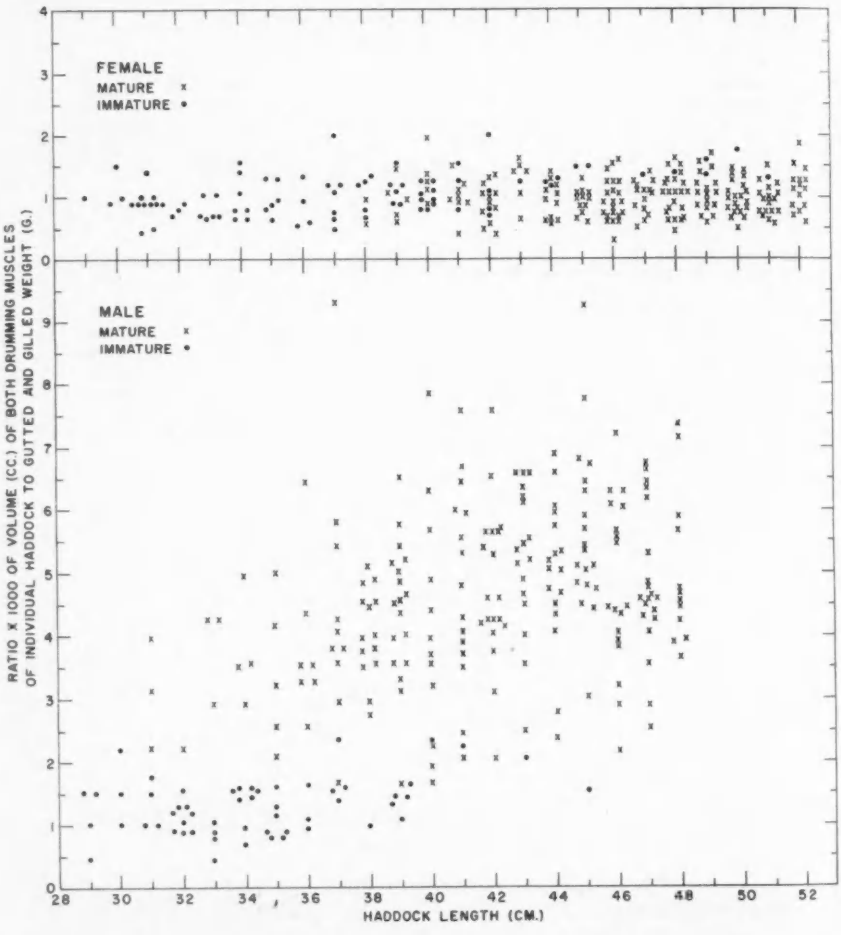

FIG. 22. Ratios ($\times$ 1000) of the volume of both drumming muscles to the gutted and gilled weight of individual mature and immature male and female haddock from the Grand Bank and St. Pierre Bank, May–June, 1956 and 1957.

and possibly delays ripening, or they may lack a drumming muscle depressant hormone associated with sexual maturity in the female. However, because of the small number of observations and the small degree of difference more observations are necessary for definite conclusions on the relative size of these drumming muscles in immature and mature females.

While there is very little overlap in the volumes of the drumming muscles

of individual immature male and mature male haddock, there is complete overlap for the immature and mature females; and there is even a good possibility (as stated above) that the larger immature females have bigger drumming muscles than mature females of the same length (Fig. 21, 22).

Since haddock recovering from their early spawnings pass through an immature-appearing condition on their way to maturity again, it was not always possible to distinguish with certainty haddock which were maturing for the first time. Some male haddock actually maturing for the first time, and yet included in the mature category, are doubtless responsible for some of the intermediate values and the lack of complete distinction between the drumming muscle volumes of immature and mature male haddock, and between mature male and mature female haddock at the smaller mature sizes, particularly in the autumn and winter.

There is little difference in the volumes of the drumming muscles in immature males and immature females (Table I–V; Fig. 21, 22). The averages for the immature males may be slightly greater but there is almost complete overlapping in individual volumes.

DETERMINATION OF SEX OF GUTTED HADDOCK BY THE SIZE AND COLOUR OF THE DRUMMING MUSCLES

In the past it has been impossible to determine the sex of most haddock landed in the gutted condition by commercial trawlers, because the ovaries (at least of mature females) and a large part or all of the testes of mature males are generally removed with other viscera at sea. It has been evident to us from the earliest observations that sexually mature males could usually be separated from females and from immature fish of both sexes by means of these drumming muscles. In a test of 80 haddock from a commercial catch, taken from the Grand Bank in November, 1957, when the male drumming muscles were close to their smallest volume, 38 were mature males, 38 mature females and 4 immature females. With all traces of the sex organs removed the haddock were then examined by the junior author, who was not present during the examination of the fish for sexual maturity. The 38 males and 41 of the 42 females were correctly distinguished. For one immature female the examiner could not decide whether it was an immature male or a female. The range of length for the sample was 37 to 59 cm. for the males and 38 to 53 cm. for the females.

The primary factor in distinguishing sexes by differences in drumming muscles is the size; colour seems to be secondary. It is obvious from the foregoing photographs, tables and figures that the sex can usually be distinguished, for mature haddock, from the size of the drumming muscles. Although on the average the drumming muscles of mature males may be darker than those of females the ranges of external colour for these muscles of males and females overlap so much that attempts to distinguish between the sexes by the colour of the drumming muscles when covered by peritoneum are subject to many errors. The redder colour of the actual drumming muscle tissue of the mature male when the peri-

toneum has been stripped away is of more assistance in distinguishing the sex of the fish. Although there is quite a distinct difference in muscle size between immature and mature male haddock, it seems impossible to separate haddock into immature and mature groups for each sex, because of the difficulty of separating the immature males from the immature and mature females. This technique of sex determination, therefore, can only be applied accurately at present to mature male and female haddock.

DISCUSSION AND CONCLUSIONS

Use of the Drumming Muscles by the Haddock

The data presented show clearly that the so-called "drumming muscles" of the male haddock swim-bladder enlarge as the males become sexually mature and for a considerable period during the growth of the male haddock, and possibly, even to the largest sizes, continue to increase in volume relative to the weight of the fish. In female haddock, on the other hand, there is no increase in the relative volume of the drumming muscles with sexual maturity and no significant increase with increase in the size of the fish.

The drumming muscles of the mature males are almost twice as large during the May–June pre-spawning and spawning period as at their approximate lowest level in October–November when the testes are recovering. On the other hand these muscles in the female show no seasonal difference.

What are the probable uses of these drumming muscles of the haddock swim-bladder? It is not necessary here to enter into an extended discussion of sound production and sound-producing organs in fishes. These matters have been well surveyed in recent papers by Fish (1954) and by Jones and Marshall (1953) and in various papers quoted by these authors. We shall mention only enough references to provide a suitable background for our discussion.

Sorensen (1884) obtained feeble movements of the swim-bladder wall in haddock and cod by stimulating the drumming muscles directly and Jones obtained similar results with these species (Jones and Marshall, 1953).

Although we can find nothing definite regarding haddock, the sound-making activities of many teleosts which possess drumming muscles have been studied (Fish, 1954; Jones and Marshall, 1953). Many cases have been described by Fish in which sounds were recognized that evidently came from vibration of the swim-bladder. In the toadfish, *Opsanus tau* (L), there are special spawning season sounds different in intensity and frequency from the usual sounds. In some of the family Sciaenidae only the males possess specially developed drumming muscles, e.g. the gray squeteague *Cynoscion regalis* (Bloch and Schneider) (Fish, 1954).

Dufossé (1874) observed that the sounds made by both males and females of the sea-horse, *Hippocampus brevirostris* Cuvier, were most intense and most frequent during the breeding period.

It is obvious from our investigations on the anatomy and the variation in

size of the so-called drumming muscles of the haddock swim-bladder that these muscles are used by mature male haddock and probably not to any comparable degree by mature female or immature male or female haddock. It is evident, also, that the organ is used chiefly or entirely by the male haddock during the spawning season.

The individual male haddock, as with groundfish generally, appears to be ripe over a much larger period than the individual females, and it is persumably capable of taking part in the fertilizing of the eggs of many females. Since the male apparently has considerable latitude in the retention of sperm until it is needed, whereas when eggs are ripe and conditions are right the female presumably will spawn, one might have expected that the female would be provided with the drumming organ so as to summon the males to a spawning act.

As far as we know the details of the spawning act in haddock have not been described but it may very well be like that described for the cod, *Gadus callarias* L., in Newfoundland by Nielsen (1892), and by Dannevig (1933) and Rollefsen (1934) for cod in Norway. Each of these authors (for details see also Templeman, 1957) describes a male and a female cod performing the spawning act together with the male underneath and reversed so that they are swimming belly to belly. This pairing and spawning occurs while the cod are swimming vigorously and the eggs and milt are mixed by the swimming motions of the caudal fins. It is thus evident that the female as well as the male cod (and presumably haddock) have some power of retaining ripe eggs preliminary to the pairing and spawning.

Templeman (1948) found in the capelin, *Mallotus villosus* (Müller), that females remained a little distance offshore from the spawning beaches in large schools containing few males. Groups of females proceeded to the spawning beaches as they ripened but many more males than females were present during the spawning on the beaches. Often over 90% of the capelin captured during the actual spawning on the beaches were males. The much more delicate females were relatively uninjured by the time they were completely spent; but the individual males, having taken part in the spawning act on the beaches over an extended period, had become badly frayed and injured in the process by their vigorous motions against the beach gravel. Also in the capelin the percentage of males taking part in the actual beach spawning always increased, sometimes by almost 50% as spawning activity built up. In actual numbers, spawning was begun by a few individuals of both sexes and gradually increased, often over several hours, to mass spawning of great numbers of individuals. It appeared to us that in this case the attraction for both sexes may have been from odours from the liberated spawning products.

It is likely, therefore, that the drumming muscles of the male haddock produce low-frequency sounds which serve as a rallying call for mature males, since these typically have sperm available at spawning time, and for such females as have ripe eggs ready for liberation. Haddock are typically in schools at spawning time and the volume of sound from a large school may be great.

It is an obvious advantage to the species in producing adequate and rapid fertilization of the eggs if, in addition to the possible pairing of individuals, large numbers of the species are liberating eggs and milt at the same time in the same place. If individual pairing does not occur a mass spawning is even more necessary.

There is an obvious field here for work on the volume and wave variety of sound in haddock at spawning and at other seasons and on the uses of such sounds. At spawning time sound production could be an aid to the identification of the size and location of haddock schools and offer some help in deciding whether haddock spawning is near bottom or often, as we suspect, in mid-water at night. If spawning often occurs in mid-water at night, when the individuals would normally be more dispersed vertically than when feeding on the bottom, the sounds produced by the drumming muscles of the males would be even more useful and necessary in rallying the individuals into a compact school.

Use of Observations on Size and Appearance of the Drumming Muscles of the Swim-bladder in Distinguishing Sex and Stage of Maturity in Gutted Haddock

Large mature males and those of intermediate size can be separated without difficulty, in almost all cases, from females and from immature males, by the great difference in size and appearance of the drumming muscles. There is difficulty only at the smallest mature male sizes, and even here there would be few errors.

Mature females cannot be separated, by observations on the drumming muscles, from immature females nor from immature males. However, invariably in immature males and usually in small mature males, the gonad or parts of it remain in the gutted fish on landing; and many immature females also have the gonad remaining. Thus the method should be of considerable assistance in sexing gutted fish and assigning maturity stages to them.

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TABLE I. Average volumes of both swim-bladder drumming muscles of immature and of mature male haddock from the Grand Bank, 1956 to 1957. (Figures in parentheses indicate number of individual haddock represented in averages.)

Haddock length	Male immature					Male mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.
cm.				ACTUAL VOLUME DRUMMING MUSCLES (*cc.*)						
29–30	...	...	0.3 (6)	...	...	...	...	...	...	...
31–32	...	...	0.3(12)	...	...	...	...	0.7 (4)	...	...
33–34	...	...	0.3(12)	...	...	...	...	1.1 (7)	...	...
35–36	...	...	0.4(10)	...	0.4 (1)	...	0.8 (1)	1.2(12)	0.8 (2)	0.6 (5)
37–38	...	0.8 (2)	0.6 (3)	...	0.4 (1)	...	1.1 (3)	1.7(23)	1.0 (8)	0.9 (9)
39–40	...	0.7 (3)	0.8 (3)	...	0.7 (1)	1.6 (5)	1.2 (5)	1.9(25)	1.4(19)	1.2(17)
41–42	...	...	...	...	0.3 (1)	2.1 (5)	2.1(10)	2.6(25)	1.6(27)	1.6(13)
43–44	...	0.6 (1)	...	...	...	2.3(31)	2.9(14)	3.3(23)	2.2(33)	2.2(13)
45–46	1.5 (1)	...	1.1 (1)	...	...	2.6(14)	2.8(24)	3.7(21)	2.4(32)	2.1 (8)
47–48	...	...	...	...	...	2.9(12)	3.6(11)	3.8(22)	2.9(17)	2.4 (3)
49–50	...	...	...	...	...	3.0 (5)	4.5 (9)	4.8(16)	3.6(10)	3.7 (2)
51–52	...	...	...	...	...	3.8 (3)	4.8 (5)	5.5(18)	3.7 (4)	2.5 (1)
53–54	...	...	...	...	...	5.3 (2)	5.5 (4)	6.4(11)	...	...
55–56	...	...	...	...	...	4.4 (2)	5.5 (2)	7.6 (4)	6.6 (1)	...
57–58	...	...	...	...	...	...	...	7.7 (8)	...	...
59–60	...	...	...	...	...	6.0 (1)	7.9 (2)	8.1 (4)	...	...
61–62	...	...	...	...	...	...	...	8.2 (1)	...	...
63–64	...	...	...	...	...	...	...	11.4 (1)	...	...
65–66	...	...	...	...	...	...	...	15.5 (1)	...	...

TABLE I (*continued*)

Haddock length	Male immature					Male mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.
cm.	RATIO OF VOLUME OF DRUMMING MUSCLES (*cc.*) TO GUTTED AND GILLED WEIGHT (*g.*)—×1000									
29–30	...	...	1.3 (6)	...	...	...	...	...	...	...
31–32	...	...	1.2(12)	...	...	...	...	2.9 (4)	...	...
33–34	...	...	1.2(12)	...	...	...	...	3.7 (7)	...	...
35–36	...	...	1.1(10)	...	1.2 (1)	...	2.6 (1)	3.7(12)	1.9 (2)	1.6 (5)
37–38	...	1.8 (2)	1.5 (3)	...	0.8 (1)	...	2.6 (3)	4.3(23)	2.3 (8)	2.1 (9)
39–40	...	1.5 (3)	1.7 (3)	...	1.5 (1)	2.9 (5)	2.9 (5)	4.1(25)	2.9(19)	2.3(17)
41–42	...	...	...	...	0.5 (1)	3.4 (5)	3.9(10)	4.8(25)	2.9(27)	2.7(13)
43–44	...	1.1 (1)	...	...	...	3.3(31)	4.5(14)	5.3(23)	3.4(33)	3.2(13)
45–46	2.0 (1)	...	1.6 (1)	...	...	3.3(14)	4.0(24)	5.2(21)	3.4(32)	2.8 (8)
47–48	...	...	...	...	...	3.3(12)	4.3(11)	4.7(22)	3.4(17)	2.9 (3)
49–50	...	...	...	...	...	3.1 (5)	4.7 (9)	5.2(16)	3.9(10)	3.7 (2)
51–52	...	...	...	...	...	3.4 (3)	4.5 (5)	5.1(18)	3.4 (4)	2.3 (1)
53–54	...	...	...	...	...	3.7 (2)	4.3 (4)	5.2(11)	...	...
55–56	...	...	...	...	...	3.0 (2)	4.2 (2)	5.8 (4)	5.0 (1)	...
57–58	...	...	...	...	...	...	...	5.2 (8)	...	...
59–60	...	...	...	...	...	3.2 (1)	4.5 (2)	4.8 (4)	...	...
61–62	...	...	...	...	...	...	...	4.5 (1)	...	...
63–64	...	...	...	...	...	...	...	5.8 (1)	...	...
65–66	...	...	...	...	...	...	...	6.8 (1)	...	...

TABLE 11. Average volumes of both swim-bladder drumming muscles of immature and of mature female haddock from the Grand Bank, 1956 to 1957. (Figures in parentheses indicate number of individual haddock represented in averages.)

Haddock length	Female immature					Female mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.
cm.				ACTUAL VOLUME DRUMMING MUSCLES (*cc.*)						
29–30	...	...	0.2 (4)	...	...	...	...	...	...	...
31–32	...	...	0.2(12)	...	0.4 (1)	...	...	...	...	...
33–34	...	...	0.3(13)	...	0.3 (3)	...	...	...	...	...
35–36	...	0.4 (1)	0.3(10)	0.4 (3)	0.4 (6)	...	...	...	...	...
37–38	...	0.4 (3)	0.4(10)	0.5 (6)	0.5 (8)	...	0.4 (4)	0.3 (2)	0.3 (1)	0.3 (1)
39–40	0.5 (2)	0.7 (6)	0.5(10)	0.5(16)	0.5(13)	0.6 (1)	0.5 (4)	0.4 (7)	0.5 (5)	0.5 (2)
41–42	0.6 (2)	0.8 (1)	0.6 (1)	0.5 (6)	0.5 (3)	0.6 (7)	0.5 (3)	0.4(16)	0.6(16)	0.5 (4)
43–44	...	0.6 (1)	0.8 (1)	0.6 (2)	0.7 (1)	0.9(22)	0.7(15)	0.6(13)	0.6(15)	0.7(11)
45–46	...	...	...	...	...	0.8(25)	0.8(18)	0.6(26)	0.7(28)	0.9(11)
47–48	...	...	...	...	...	0.9(11)	0.8(27)	0.7(24)	0.8(31)	0.9 (9)
49–50	...	0.8 (1)	...	...	...	1.0 (3)	1.1 (7)	0.8(23)	1.0(17)	0.9 (3)
51–52	...	...	...	...	...	1.2 (4)	1.1 (9)	0.9(15)	1.2(10)	...
53–54	...	...	...	...	...	1.3 (3)	1.1 (4)	1.2(12)	1.8 (3)	1.2 (1)
55–56	...	...	...	...	...	...	...	1.3(10)	...	...
57–58	...	...	...	...	...	1.5 (1)	1.8 (4)	1.4 (7)	1.0 (1)	...
59–60	...	...	...	...	...	2.3 (1)	1.4 (4)	1.4 (7)	3.2 (1)	...
61–62	...	...	...	...	...	...	...	1.8 (4)	...	...
63–64	...	...	...	...	...	...	2.5 (3)	2.6 (2)	...	...
65–66	...	...	...	...	...	3.1 (1)	...	1.7 (1)	...	...
67–68	...	...	...	...	...	...	...	2.3 (2)	...	...
69–70	...	...	...	...	...	...	...	...	...	...
71–72	...	...	...	...	...	...	...	2.4 (2)	...	...

TABLE II (*continued*)

Haddock length	Female immature					Female mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Nov.
cm.	RATIO OF VOLUME OF DRUMMING MUSCLES (*cc.*) TO GUTTED AND GILLED WEIGHT (g.)—×1000.									
29–30	...	...	1.1 (4)	...	...	...	...	...	...	...
31–32	...	...	0.9(12)	...	1.6 (1)	...	...	...	...	...
33–34	...	...	0.9(13)	...	1.0 (3)	...	...	...	...	...
35–36	...	1.3 (1)	0.9(10)	1.1 (3)	1.0 (6)	...	...	...	...	...
37–38	...	1.0 (3)	1.2(10)	1.2 (6)	1.1 (8)	...	1.0 (4)	0.8 (2)	0.8 (1)	0.7 (1)
39–40	0.9 (2)	1.5 (6)	1.0(10)	0.9(16)	1.0(13)	1.1 (1)	1.1 (4)	1.0 (7)	0.9 (5)	0.8 (2)
41–42	1.1 (2)	1.6 (1)	1.1 (1)	0.9 (6)	0.9 (3)	1.1 (7)	1.0 (3)	0.9(16)	1.0(16)	0.8 (4)
43–44	...	0.9 (1)	1.2 (1)	0.9 (2)	1.1 (1)	1.3(22)	1.1(15)	1.0(13)	0.9(15)	1.0(11)
45–46	...	...	...	...	...	1.0(25)	1.1(18)	0.9(26)	1.0(28)	1.1(11)
47–48	...	...	...	...	...	1.1(11)	1.0(27)	0.9(24)	1.0(31)	1.1 (9)
49–50	...	1.0 (1)	...	...	...	1.1 (3)	1.2 (7)	1.0(23)	1.1(17)	0.9 (3)
51–52	...	...	...	...	...	1.0 (4)	1.1 (9)	1.0(15)	1.1(10)	...
53–54	...	...	...	...	...	1.1 (3)	0.9 (4)	1.0(12)	1.6 (3)	1.0 (1)
55–56	...	...	...	...	...	...	...	1.0(10)	...	...
57–58	...	...	...	...	...	1.0 (1)	1.2 (4)	1.0 (7)	0.7 (1)	...
59–60	...	...	...	...	...	1.2 (1)	0.9 (4)	0.9 (7)	2.0 (1)	...
61–62	...	...	...	...	...	...	...	1.0 (4)	...	...
63–64	...	...	...	...	...	...	1.3 (3)	1.2 (2)	...	...
65–66	...	...	...	...	...	1.4 (1)	...	0.8 (1)	...	...
67–68	...	...	...	...	...	...	...	1.1 (2)	...	...
69–70	...	...	...	...	...	...	...	...	...	...
71–72	...	...	...	...	...	...	...	0.9 (2)	...	...

TABLE III. Average volumes of both swim-bladder drumming muscles of immature and of mature male and female haddock from St. Pierre Bank, 1956 to 1957. (Figures in parentheses indicate number of individual haddock represented in averages.)

Haddock length	Immature male		Mature male		Immature female		Mature female	
	June	Oct.	June	Oct.	June	Oct.	June	Oct.
cm.			ACTUAL VOLUME DRUMMING MUSCLES (*cc.*)					
29–30	0.3(1)	...	...	...	...	...	...	...
31–32	0.2(1)	0.3(3)	...	...	0.2(2)	0.4(1)	...	...
33–34	...	...	...	0.4(2)	...	0.3(3)	...	...
35–36	...	...	...	0.6(1)	...	0.5(2)	...	...
37–38	0.7(2)	...	1.5 (1)	0.8(3)	0.3(2)	...	...	...
39–40	0.6(3)	...	2.6 (5)	1.3(1)	0.6(5)	0.6(8)	0.8 (3)	...
41–42	1.4(1)	...	2.7 (9)	2.1(3)	0.7(6)	0.7(5)	0.7 (4)	0.6(2)
43–44	1.4(1)	...	3.4(11)	1.7(5)	0.8(3)	0.7(2)	0.9 (4)	0.7(7)
45–46	...	...	4.1(16)	2.4(4)	1.1(2)	0.9(1)	0.8 (8)	1.1(7)
47–48	...	...	5.0(10)	2.4(4)	1.2(2)	...	1.1(12)	1.0(8)
49–50	...	...	5.8 (9)	2.8(5)	1.6(3)	...	1.1(15)	1.2(4)
51–52	...	...	5.5 (7)	3.2(4)	1.5(1)	...	1.2(17)	1.4(3)
53–54	...	...	7.0 (6)	4.3(1)	2.1(1)	...	1.4(18)	1.4(5)
55–56	...	...	8.2 (8)	...	...	...	1.6 (9)	...
57–58	...	...	11.7 (9)	7.3(1)	...	...	2.2 (5)	...
59–60	...	...	12.9 (8)	5.2(1)	...	...	1.9 (2)	1.4(1)
61–62	...	...	12.9 (5)	...	...	...	2.8 (5)	2.6(1)
63–64	...	...	15.4 (4)	6.5(1)	...	...	2.7 (4)	2.5(1)
65–66	...	...	16.2(10)	...	...	...	2.9 (2)	...
67–68	...	...	14.5 (4)	...	...	...	2.8 (3)	...
69–70	...	...	20.0 (2)	...	...	...	4.1 (4)	...
71–72	...	...	...	...	...	...	4.1 (3)	...
73–74	...	...	...	....	...	...	3.8 (2)	...
75–76	...	...	31.0 (1)	...	...	...	3.0 (1)	2.6(1)

TABLE III (*continued*)

Haddock length	Immature male		Mature male		Immature female		Mature female	
	June	Oct.	June	Oct.	June	Oct.	June	Oct.
cm.	RATIO OF VOLUME OF DRUMMING MUSCLES (*cc.*) TO GUTTED AND GILLED WEIGHT (*g.*)—× 1000							
29–30	1.5(1)	...	...	...	...	...	...	...
31–32	1.0(1)	1.3(3)	...	...	0.7(2)	1.6(1)	...	...
33–34	...	...	...	1.5(2)	...	1.1(3)	...	...
35–36	...	...	...	1.6(1)	...	1.3(2)	...	...
37–38	1.7(2)	...	2.9 (1)	2.2(3)	0.6(2)	...	...	...
39–40	1.4(3)	...	5.1 (5)	2.4(1)	1.1(5)	1.1(8)	1.5 (3)	...
41–42	2.2(1)	...	4.8 (9)	3.7(3)	1.2(6)	1.3(5)	1.2 (4)	0.9(2)
43–44	2.1(1)	...	4.9(11)	2.7(5)	1.3(3)	1.1(2)	1.3 (4)	1.1(7)
45–46	...	...	5.3(16)	3.1(4)	1.5(2)	1.2(1)	1.1 (8)	1.4(7)
47–48	...	...	5.4(10)	2.8(4)	1.4(2)	...	1.2(12)	1.1(8)
49–50	...	...	5.8 (9)	2.8(5)	1.6(3)	...	1.1(15)	1.3(4)
51–52	...	...	5.0 (7)	2.9(4)	1.3(1)	...	1.1(17)	1.3(3)
53–54	...	...	5.6 (6)	3.8(1)	1.6(1)	...	1.1(18)	1.1(5)
55–56	...	...	5.7 (8)	...	...	...	1.2 (9)	...
57–58	...	...	7.1 (9)	4.5(1)	...	...	1.5 (5)	...
59–60	...	...	7.2 (8)	3.0(1)	...	...	1.1 (2)	0.8(1)
61–62	...	...	6.5 (5)	...	...	...	1.5 (5)	1.5(1)
63–64	...	...	7.2 (4)	3.3(1)	...	...	1.3 (4)	1.4(1)
65–66	...	...	7.0(10)	...	...	...	1.2 (2)	...
67–68	...	...	5.9 (4)	...	...	...	1.1 (3)	...
69–70	...	...	7.5 (2)	...	...	...	1.6 (4)	...
71–72	...	...	...	...	...	...	1.5 (3)	...
73–74	...	...	...	...	...	...	1.2 (2)	...
75–76	...	...	8.7 (1)	...	...	...	1.0 (1)	0.9(1)

TABLE IV. Average volumes of both swim-bladder drumming muscles of immature and of mature male haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957. (Figures in parentheses indicate number of individual haddock represented in averages.)

Haddock length	Male immature					Male mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.
cm.				ACTUAL VOLUME DRUMMING MUSCLES (*cc.*)						
29–30	...	...	0.3 (7)	...	...	...	...	...	...	...
31–32	...	...	0.3(13)	...	0.3 (3)	...	...	0.7 (4)	...	...
33–34	...	...	0.3(12)	...	...	...	...	1.1 (7)	...	0.4 (2)
35–36	...	...	0.4(10)	...	0.4 (1)	...	0.8 (1)	1.2(12)	0.8 (2)	0.6 (6)
37–38	...	0.8 (2)	0.6 (5)	...	0.4 (1)	...	1.1 (3)	1.7(24)	1.0 (8)	0.9(12)
39–40	...	0.7 (3)	0.7 (6)	...	0.7 (1)	1.6 (5)	1.2 (5)	2.0(30)	1.4(19)	1.2(18)
41–42	...	...	1.4 (1)	...	0.3 (1)	2.1 (5)	2.1(10)	2.7(34)	1.6(27)	1.7(16)
43–44	...	0.6 (1)	1.4 (1)	...	...	2.3(31)	2.9(14)	3.3(34)	2.2(33)	2.0(18)
45–46	1.5 (1)	...	1.1 (1)	...	...	2.6(14)	2.8(24)	3.8(37)	2.4(32)	2.2(12)
47–48	...	...	...	...	...	2.9(12)	3.6(11)	4.1(32)	2.9(17)	2.4(7)
49–50	...	...	...	...	...	3.0 (5)	4.5 (9)	5.2(25)	3.6(10)	3.1 (7)
51–52	...	...	...	...	...	3.8 (3)	4.8 (5)	5.5(25)	3.7 (4)	3.1 (5)
53–54	...	...	...	...	...	5.3 (2)	5.5 (4)	6.6(17)	...	4.3 (1)
55–56	...	...	...	...	...	4.4 (2)	5.5 (2)	8.0(12)	6.6 (1)	...
57–58	...	...	...	...	...	...	...	9.8(17)	...	7.3 (1)
59–60	...	...	...	...	...	6.0 (1)	7.9 (2)	11.3(12)	...	5.2 (1)
61–62	...	...	...	...	...	...	...	12.1 (6)	...	...
63–64	...	...	...	...	...	...	...	14.6 (5)	...	6.5 (1)
65–66	...	...	...	...	...	...	...	16.2(11)	...	...
67–68	...	...	...	...	...	...	...	14.5 (4)	...	...
69–70	...	...	...	...	...	...	...	20.0 (2)	...	...
75–76	...	...	...	...	...	...	...	31.0 (1)	...	...

TABLE IV (*continued*)

Haddock length	Male immature					Male mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.
cm.	RATIO OF VOLUME OF DRUMMING MUSCLES (*cc.*) TO GUTTED AND GILLED WEIGHT (*g.*)—× 1000.									
29–30	...	...	1.3 (7)	...	...	...	...	...	...	...
31–32	...	...	1.2(13)	...	1.3 (3)	...	...	2.9 (4)	...	...
33–34	...	...	1.2(12)	...	...	...	...	3.7 (7)	...	1.5 (2)
35–36	...	...	1.1(10)	...	1.2 (1)	...	2.6 (1)	3.7(12)	1.9 (2)	1.6 (6)
37–38	...	1.8 (2)	1.6 (5)	...	0.8 (1)	...	2.6 (3)	4.2(24)	2.3 (8)	2.1(12)
39–40	...	1.5 (3)	1.6 (6)	...	1.5 (1)	2.9 (5)	2.9 (5)	4.3(30)	2.9(19)	2.3(18)
41–42	...	...	2.2 (1)	...	0.5 (1)	3.4 (5)	3.9(10)	4.8(34)	2.9(27)	2.9(16)
43–44	...	1.1 (1)	2.1 (1)	...	...	3.3(31)	4.5(14)	5.1(34)	3.4(33)	3.1(18)
45–46	2.0 (1)	...	1.6 (1)	...	...	3.3(14)	4.0(24)	5.2(37)	3.4(32)	2.9(12)
47–48	...	...	...	...	...	3.3(12)	4.3(11)	4.9(32)	3.4(17)	2.9(7)
49–50	...	...	...	...	...	3.1 (5)	4.7 (9)	5.4(25)	3.9(10)	3.1 (7)
51–52	...	...	...	...	...	3.4 (3)	4.5 (5)	5.1(25)	3.4 (4)	2.8 (5)
53–54	...	...	...	...	...	3.7 (2)	4.3 (4)	5.4(17)	...	3.8 (1)
55–56	...	...	...	...	...	3.0 (2)	4.2 (2)	5.7(12)	5.0 (1)	...
57–58	...	...	...	...	...	...	...	6.2(17)	...	4.5 (1)
59–60	...	...	...	...	...	3.2 (1)	4.5 (2)	6.4(12)	...	3.0 (1)
61–62	...	...	...	...	...	...	...	6.1 (6)	...	...
63–64	...	...	...	...	...	...	...	6.9 (5)	...	3.3 (1)
65–66	...	...	...	...	...	...	...	7.0(11)	...	...
67–68	...	...	...	...	...	...	...	5.9 (4)	...	...
69–70	...	...	...	...	...	...	...	7.5 (2)	...	...
75–76	...	...	...	...	...	...	...	8.7 (1)	...	...

TABLE V. Average volumes of both swim-bladder drumming muscles of immature and of mature female haddock from the Grand Bank and St. Pierre Bank, 1956 to 1957. (Figures in parentheses represent number of individual haddock represented in averages.)

Haddock length	Female immature					Female mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.
cm.				ACTUAL VOLUME DRUMMING MUSCLES (*cc.*)						
29–30	...	...	0.2 (4)	...	...	...	...	...	...	...
31–32	...	...	0.2(14)	...	0.4 (2)	...	...	...	...	...
33–34	...	...	0.3(13)	...	0.3 (6)	...	...	...	...	...
35–36	...	0.4 (1)	0.3(10)	0.4 (3)	0.4 (8)	...	...	...	...	...
37–38	...	0.4 (3)	0.4(12)	0.5 (6)	0.5 (8)	...	0.4 (4)	0.3 (2)	0.3 (1)	0.3 (1)
39–40	0.5 (2)	0.7 (6)	0.5(15)	0.5(16)	0.5(21)	0.6 (1)	0.5 (4)	0.6(10)	0.5 (5)	0.5 (2)
41–42	0.6 (2)	0.8 (1)	0.7 (7)	0.5 (6)	0.7 (8)	0.6 (7)	0.5 (3)	0.5(20)	0.6(16)	0.6 (6)
43–44	...	0.6 (1)	0.8 (4)	0.6 (2)	0.7 (3)	0.9(22)	0.7(15)	0.7(17)	0.6(15)	0.7(18)
45–46	...	...	1.1 (2)	...	0.9 (1)	0.8(25)	0.8(18)	0.7(34)	0.7(28)	0.9(18)
47–48	...	...	1.2 (2)	...	...	0.9(11)	0.8(27)	0.8(36)	0.8(31)	1.0(17)
49–50	...	0.8 (1)	1.6 (3)	...	...	1.0 (3)	1.1 (7)	0.9(38)	1.0(17)	1.1 (7)
51–52	...	...	1.5 (1)	...	...	1.2 (4)	1.1 (9)	1.1(32)	1.2(10)	1.4 (3)
53–54	...	...	2.1 (1)	...	...	1.3 (3)	1.1 (4)	1.3(30)	1.8 (3)	1.4 (6)
55–56	...	...	...	...	...	...	...	1.5(19)	...	...
57–58	...	...	...	...	...	1.5 (1)	1.8 (4)	1.7(12)	1.0 (1)	...
59–60	...	...	...	...	...	2.3 (1)	1.4 (4)	1.5 (9)	3.2 (1)	1.4 (1)
61–62	...	...	...	...	...	...	...	2.4 (9)	...	2.6 (1)
63–64	...	...	...	...	...	...	2.5 (3)	2.6 (6)	...	2.5 (1)
65–66	...	...	...	...	...	3.1 (1)	...	2.5 (3)	...	...
67–68	...	...	...	...	...	...	...	2.6 (5)	...	...
69–70	...	...	...	...	...	...	...	4.1 (4)	...	...
71–72	...	...	...	...	...	...	...	3.4 (5)	...	...
73–74	...	...	...	...	...	...	...	3.8 (2)	...	...
75–76	...	...	...	...	...	...	...	3.0 (1)	...	2.6 (1)

TABLE V (*continued*)

Haddock length	Female immature					Female mature				
	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.	Jan.	Mar.–Apr.	May–June	Aug.–Sept.	Oct.–Nov.
cm.	RATIO OF VOLUME OF DRUMMING MUSCLES (*cc.*) TO GUTTED AND GILLED WEIGHT (g.)—×1000									
29–30	...	...	1.1 (4)	...	...	...	...	...	...	...
31–32	...	...	0.9(14)	...	1.6 (2)	...	...	...	...	...
33–34	...	...	0.9(13)	...	1.1 (6)	...	...	...	...	...
35–36	...	1.3 (1)	0.9(10)	1.1 (3)	1.0 (8)	...	...	...	...	...
37–38	...	1.0 (3)	1.1(12)	1.2 (6)	1.1 (8)	...	1.0 (4)	0.8 (2)	0.8 (1)	0.7 (1)
39–40	0.9 (2)	1.5 (6)	1.1(15)	0.9(16)	1.0(21)	1.1 (1)	1.1 (4)	1.1(10)	0.9 (5)	0.8 (2)
41–42	1.1 (2)	1.6 (1)	1.2 (7)	0.9 (6)	1.1 (8)	1.1 (7)	1.0 (3)	0.9(20)	1.0(16)	0.9 (6)
43–44	...	0.9 (1)	1.3 (4)	0.9 (2)	1.1 (3)	1.3(22)	1.1(15)	1.1(17)	0.9(15)	1.0(18)
45–46	...	...	1.5 (2)	...	1.2 (1)	1.0(25)	1.1(18)	0.9(34)	1.0(28)	1.2(18)
47–48	...	...	1.4 (2)	...	...	1.1(11)	1.0(27)	1.0(36)	1.0(31)	1.1(17)
49–50	...	1.0 (1)	1.6 (3)	...	...	1.1 (3)	1.2 (7)	1.0(38)	1.1(17)	1.1 (7)
51–52	...	...	1.3 (1)	...	...	1.0 (4)	1.1 (9)	1.0(32)	1.1(10)	1.3 (3)
53–54	...	...	1.6 (1)	...	...	1.1 (3)	0.9 (4)	1.1(30)	1.6 (3)	1.1 (6)
55–56	...	...	...	...	...	...	...	1.1(19)	...	...
57–58	...	...	...	...	...	1.0 (1)	1.2 (4)	1.2(12)	0.7 (1)	...
59–60	...	...	...	...	...	1.2 (1)	0.9 (4)	0.9 (9)	2.0 (1)	0.8 (1)
61–62	...	...	...	...	...	...	...	1.3 (9)	...	1.5 (1)
63–64	...	...	...	...	...	...	1.3 (3)	1.3 (6)	...	1.4 (1)
65–66	...	...	...	...	...	1.4 (1)	...	1.1 (3)	...	...
67–68	...	...	...	...	...	...	...	1.1 (5)	...	...
69–70	...	...	...	...	...	...	...	1.6 (4)	...	...
71–72	...	...	...	...	...	...	...	1.2 (5)	...	...
73–74	...	...	...	...	...	...	...	1.2 (2)	...	...
75–76	...	...	...	...	...	...	...	1.0 (1)	...	0.9 (1)

TABLE VI. Average volumes of both drumming muscles of immature and of mature female haddock from the Grand Bank and St. Pierre Bank, January, 1956 to September, 1957. (Figures in parentheses indicate number of individual haddock represented in averages.)

Haddock length	Av. vol. drumming muscles		Av. ratio (×1000) of vol. drumming muscles (*cc.*) to gutted and gilled weight (g.)	
	Immature female	Mature female	Immature female	Mature female
cm.	*cc.*	*cc.*		
29–30	0.23 (4)	...	1.11 (4)	...
31–32	0.22(16)	...	0.95(16)	...
33–34	0.27(19)	...	0.95(19)	...
35–36	0.36(22)	...	1.01(22)	...
37–38	0.45(29)	0.35 (8)	1.10(29)	0.89 (8)
39–40	0.51(60)	0.52 (22)	1.05(60)	1.05 (22)
41–42	0.63(24)	0.55 (52)	1.10(24)	0.96 (52)
43–44	0.71(10)	0.72 (87)	1.08(10)	1.08 (87)
45–46	1.03 (3)	0.75(123)	1.39 (3)	1.01(123)
47–48	1.20 (2)	0.84(122)	1.37 (2)	1.03(122)
49–50	1.43 (4)	0.98 (72)	1.42 (4)	1.06 (72)
51–52	1.50 (1)	1.12 (58)	1.29 (1)	1.05 (58)
53–54	2.10 (1)	1.31 (46)	1.61 (1)	1.09 (46)
55–56	...	1.46 (19)	...	1.09 (19)
57–58	...	1.69 (18)	...	1.17 (18)
59–60	...	1.63 (16)	...	1.00 (16)

The Evolution of Migratory Behaviour among Juvenile Salmon of the Genus *Oncorhynchus*[1,2]

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ABSTRACT

The discussion is based on a detailed ethological comparison of four species of juvenile *Oncorhynchus*—coho, chum, sockeye and pink salmon. Their behaviour is described in terms of five fixed behaviour patterns—hiding under stones, occupying territories, schooling, feeding and escaping predators. These are performed in relation to five directive factors—light, temperature, current, salinity and objects in the environment. Behaviour patterns and directing factors are associated with characteristic appetitive behaviour. The internal motivation seems to have an endocrinological basis. The coho fry, because of its river habitat, territorial behaviour, low nocturnal activity and smolt transformation, is considered to show behaviour nearest to that of the parental type of the genus. The pink fry has the most highly specialized sea-going behaviour. Three major developments are evident in the evolution of obligatory pelagic and ocean dwelling species (a) early smolt transformation (b) increased nocturnal activity and (c) schooling. Some possible evolutionary sequences are considered.

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INTRODUCTION

THE AVAILABLE EVIDENCE indicates that the Salmonidae have evolved from freshwater ancestors. Although no direct palaeontological records of salmonids have yet been found, studies of their anatomy, ecology, distribution and physiology support best the concept of a freshwater origin. Tchernavin (1939) summarized the different arguments and concluded that "the ancestors of the Salmonidae from early Eocene onwards were probably freshwater fish, and only during the glacial period, when all the recent species of this family already existed, did some of them acquire migratory habits". The same arguments support the idea that the ancestral salmonids were trout-like in their form and habits and that the genus of Pacific salmon, *Oncorhynchus*—with its strongly developed sea-going habits—represents an extreme in the phylogeny of migratory behaviour within this family.

The salmon is able to travel hundreds of miles through unfamiliar rivers, lakes and oceans and to return again to fresh waters—frequently to those of its parent stream. The time sequence and details of the phylogeny of this migratory behaviour are unknown but it is possible to reconstruct some parts of the story from careful comparative studies of the many existing species of this large family. In the present paper an attempt is made to develop a picture of the evolution of downstream migratory behaviour in the juveniles of Pacific salmon. This analysis is based on a comparative ethological study of four species of *Oncorhynchus*—the coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*) and pink (*O. gorbuscha*).

Migratory behaviour is a characteristic feature of the biology of the genus *Oncorhynchus*. Of the five North American species, only one—the sockeye—normally completes its entire life cycle in fresh water and maintains self-perpetuating fresh water populations. Even the sockeye assumes a lake habitat and a pelagic schooling behaviour rather than the river habitat and solitary behaviour of bottom dwelling forms such as the more primitive trout and char. The other North American species of Pacific salmon are obliged to enter sea water in order to complete successfully their life history. Yet within the genus, the stream-dwelling trout-like behaviour is clearly evident in some species at certain times. The comparison of the juvenile behaviour patterns suggests something of the evolution from this type of behaviour to obligatory seaward migrants such as the pink salmon which must enter sea water at an early stage or perish.

The discussion is primarily based on studies of the recently emerged fry. These little fish, as they appear to the writer, are shown in Figure 1. In general, they all hatch during the spring from eggs which have been deposited in the stones and gravel of rivers, although, in some places, the sockeye spawn in lakes. Coho normally live a year or longer in the rivers (sometimes in lakes) before undergoing a morphological and physiological transformation (*smolt transformation*) and taking up residence in the ocean. The sockeye enter lakes shortly after hatching and live a pelagic life for a year or more prior to their smolt transformation and journey to the sea. The chums and pinks, for most of their lives, are obligatory ocean dwellers and migrate to the sea soon after emerging from the gravel.

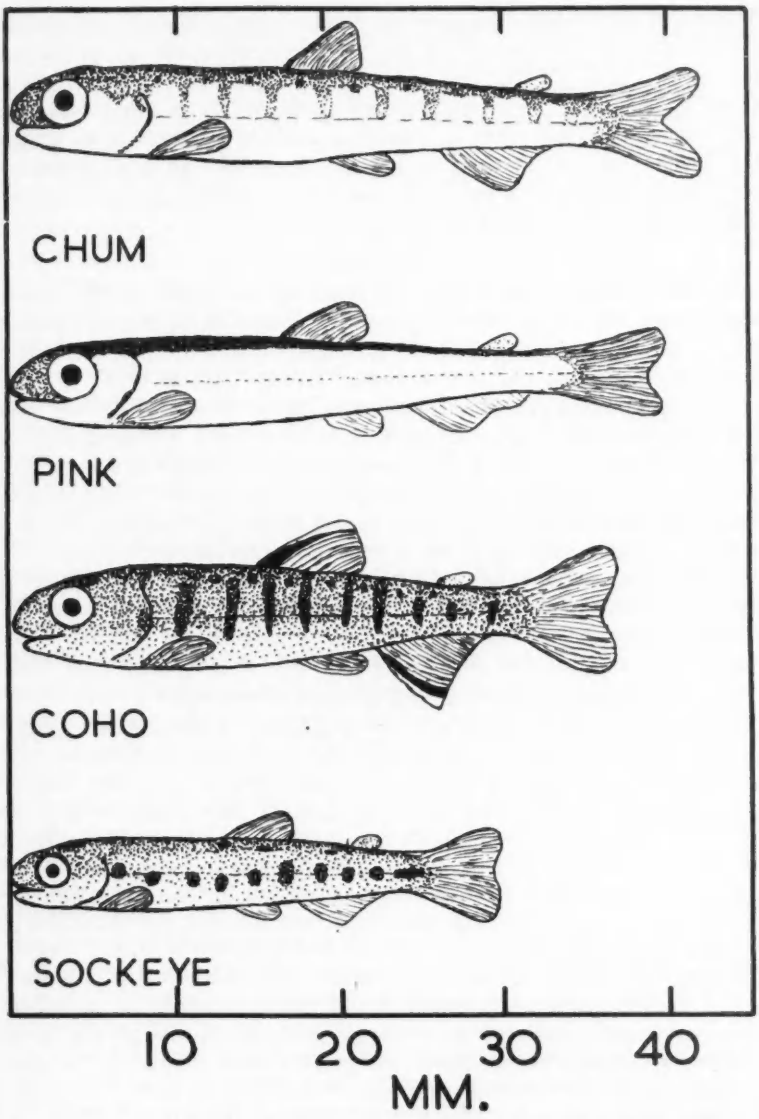

FIG. 1. Diagram showing the external distinguishing features of four species of Pacific salmon fry as they appear to the writer.

Many of the findings discussed here have been published previously, and the observed activities related to the migratory behaviour of young salmon (Hoar, 1951, 1954, 1956). The possible phylogenetic relationships of these patterns of behaviour, however, were not at all evident in the earlier years of the investigation. In this paper an attempt is made to catalogue more completely the behaviour patterns of the four species as juveniles in fresh water and to show how the different activities have become specialized during the evolution of the migratory behaviour of the genus *Oncorhynchus*.

METHODS

The first of these observations was made at the Departure Bay laboratory of the Fisheries Research Board, at Nanaimo, during the spring and summer of 1949. They were continued at the Board's field stations at Nile Creek in 1950, at Port John in 1951–52 and 1955–57 and at Lakelse Lake in 1953.

The experimental procedures are simple. Small groups of fish are watched in readily observable areas such as aquaria or troughs. Detailed descriptions of their activities with quantitative records of their distribution form the raw data. During the first four seasons, fish were studied indoors under subdued or artificial light. Subsequently the apparatus was placed under outdoor illumination —usually in shallow running water in order to maintain temperatures.

It should be emphasized that the same activities are observed both in the laboratory and out of doors. The salmon's repertoire of behaviour is limited and the same behaviour patterns will be seen wherever the fish are watched. However, the interpretation of these activities is a different matter and it is only when the observations are repeated many times under a wide variety of conditions that their significance can be evaluated. In the present study large aquaria succeeded smaller ones; long troughs and circular channels followed short troughs and tubs. Finally, the entire picture—as it is now developed—could be seen in a long trough of running water with dark background and bottom partially covered with stones and gravel. The limitations in the earlier work, however, were only partly in the apparatus, and an understanding of what is seen in the long trough (or the stream) grew out of the recognition of what the fish were doing in the more unnatural environments. The activities themselves can never be considered "un-natural" but an understanding of their meaning depends on repeated observations under many and varied conditions.

Any patient observer can readily see all the activities to be described. He will also see numerous exceptions to the general rules. An animal's behaviour is one of its most variable characteristics and predictions of what it may be expected to do at any particular moment are subject to considerable error. This variability makes concise descriptions difficult. It is, however, the same variability which enables the salmon to survive in a highly changeable environment and which permitted the genus *Oncorhynchus* to evolve its varied and efficient mechanisms of downstream migration.

INSTINCTIVE ACTIVITIES OF JUVENILE PACIFIC SALMON

To the ethologist, the activities of a fish may be separated into a limited number of discrete behaviour patterns. These are normally set in motion by

specific environmental situations (releasers) such as odours, visual pictures or mechanical stimuli. They are specific to each species and are inherited as a group of self-differentiating muscular movements, quite as characteristic of the species as any of its morphological features. These behaviour patterns are oriented in the world where the fish lives by gradients of light, temperature, current or the local geography. A characteristic internal as well as external environment is essential to the expression of this instinctive behaviour. Many of the behaviour patterns appear only when the animal is in a particular physiological condition (hungry, sexually mature).

In addition to the fixed behaviour patterns and their steering components, the concept of "appetitive behaviour" forms an essential part of the ethological analysis. An appropriate internal state (hunger, sexual maturity) may develop in the absence of the environmental releaser (food, a mate). The locomotor activity which is characteristic of this situation is referred to as "appetitive behaviour". It may be either random or oriented with respect to environmental gradients or other factors in the environment. More detailed accounts of current ethological theory will be found in discussions by Tinbergen (1951) and Baerends (1957). The meagre outline given above will serve for present purposes, and the behaviour of the juvenile Pacific salmon will now be described within this framework of ethological thinking. A catalogue of the behaviour patterns will be followed by discussion of their steering components (Baerends, 1957), the associated appetitive behaviour and the variable internal environment. Possible phylogenetic relationships will then be considered.

THE FIXED BEHAVIOUR PATTERNS

Young Pacific salmon are almost constantly in motion. The number of different things which they do, however, is small and the movements simple in comparison with some of the activities of mature fish. Five distinct behaviour patterns are recognized. All of the activities observed in this investigation can be described within this framework of five complex movements with their associated steering factors and appetitive behaviour.

(*a*) Hiding under Stones

This seems to be the complete behaviour of the newly hatched salmon alevin. In the yolk-sac stages the young fish press into small cracks or crevices and hide in dark corners or under rocks. If there is no such shelter they will swim closely together in the darkest corner of the tank. This behaviour of hiding probably persists to some measure throughout the life of all species—at least when individuals are isolated and alarmed. Species variations are, however, marked. When the yolk sac is largely or completely absorbed hiding behaviour disappears in all species at very low light intensity. At higher light intensities groups of sockeye fry still hide almost continuously for several weeks or months after first emerging while this behaviour disappears almost entirely as soon as the pink fry emerges and schools. Recently emerged coho and chum salmon represent intermediate conditions.

The best demonstrations of this behaviour in the recently emerged fry were seen when groups of 100 fish were studied in troughs of running water

(length 360 cm.) containing two areas of stones and gravel which separated three equally spaced pools. The interiors of the troughs were painted with black asphalt varnish and covered with a thin layer of sand. Detailed descriptions and an illustration have been published (Hoar, 1956).

Group of 100 sockeye fry placed in this environment either during the day or night are seen in only small numbers during the day. The maximum numbers observed over a period of three weeks (six different groups) during the day (light intensities between 100 and 3,000 foot-candles) was 24% while usually fewer than 10% were seen. Frequently no fish were exposed when the trough was examined. In the evening, however, when the light intensity falls below 50 ft.-c. (more often below 10 ft.-c.) they emerge in large numbers, which cannot readily be counted, and swim to and fro in schools from one end of the trough to the other. Older post-migrant sockeye fry lose (by midsummer) this behaviour of continuously hiding under stones (Hoar, Keenleyside and Goodall, 1957).

The recently emerged pink fry has a behaviour markedly different from that of the sockeye under similar circumstances. Althought pink fry which have never schooled prefer a cover of stones and do not emerge into bright (outdoor) light, those which have schooled remain in the light unless the change is rapid and of considerable magnitude. This has been demonstrated by collecting groups of migrating pink fry in the darkness from a counting weir and comparing their reactions with those of groups collected in the same manner but permitted to school for ten minutes under an artificial light. Fewer than 50% of the unschooled fish emerged from the gravel on the following day while 75% to 80% of the schooled fish were found (Hoar, 1956).

Similar differences between schooled and unschooled pinks have been demonstrated in another way. Pink fry, presumably with little or no schooling experience, were again collected individually from the screens of the counting weir at midnight. They were placed individually in paper drinking cups (450 ml. capacity). At the same time, an equal number of fry were isolated to similar paper cups from a school of 100 fish collected the previous evening. To control temperature both groups were kept in a bath of running water until their responses were compared the next morning (period of 8 to 12 hours). Their hiding behaviour was studied in aluminium-painted galvanized iron buckets of water (top diameter 32.5 cm., bottom diameter 29 cm., depth 21 cm.) with stones to a depth of about 12 cm. The buckets were placed under a shelter where the light intensity was approximately 65 ft.-c.

Fish were placed individually in the buckets at 30-second intervals until a group of 12 had been added. In doing this, the contents of the paper cup were poured through a wire net and the fish then dumped into the test bucket. Number of fish evident above the stones was recorded at intervals of two to three minutes for a period of 20 minutes.

Differences in the responses of the two groups were obvious. Unschooled pink fry quickly disappeared into the stones, so that two or fewer fish were evident when the last individual was added (5.5 min.). The reaction was much

less marked with the schooled fish and as many as half of the sample was regularly present when the last individual was added. In both groups the number in sight increased regularly over the 20-minute period (Fig. 2). The quantitative data are based on a comparison of eleven different groups, or a total of 130 fish (two tests with 11 instead of 12 individuals). At the end of 20 minutes 81.5% of the schooled fish had appeared, in comparison with 48.5% of the unschooled individuals.

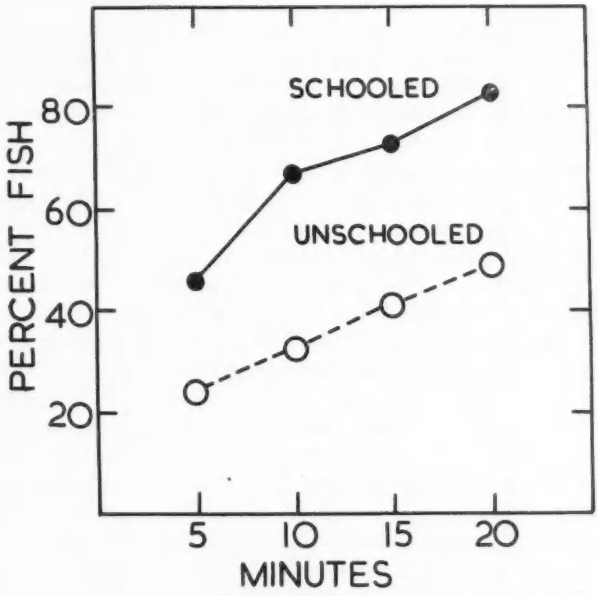

FIG. 2. Percentage of pink fry appearing at various intervals after being placed in test buckets; 130 pink fry are involved in each group.

It may be asked why any of the unschooled fry appear. The area is small; the fish are active; light intensity is low and individual fish in wandering about come together and swim up in small groups which gradually increase in number. Perhaps even more significant is the absence of a current in the water since it will be shown in another section that current has a strong orienting effect in the hiding of all species. It should also be added that there is no absolute proof that *all* of the "unschooled" fish lacked schooling experience.

The disappearance of some of the schooled fish may also be questioned in the light of experiments described below. In this connection it should be recalled that these "schooled" individuals had been isolated into the paper cups for a period of seven or more hours. It was shown in another series of experiments, carried out in the same manner, that some waning of the school-

ing response does occur during this interval (Fig. 3) and that pink fry immediately after separation from a school do not disappear at all under these conditions (Fig. 5).

The reactions of chum fry are very different when studied in comparable tests. Chums were likewise collected from the screens of the fish weir, placed individually in paper cups and their reactions compared in a manner identical with that just described for pink fry. Because of the nature of the response, as described below, it was not necessary to compare schooled chum fry.

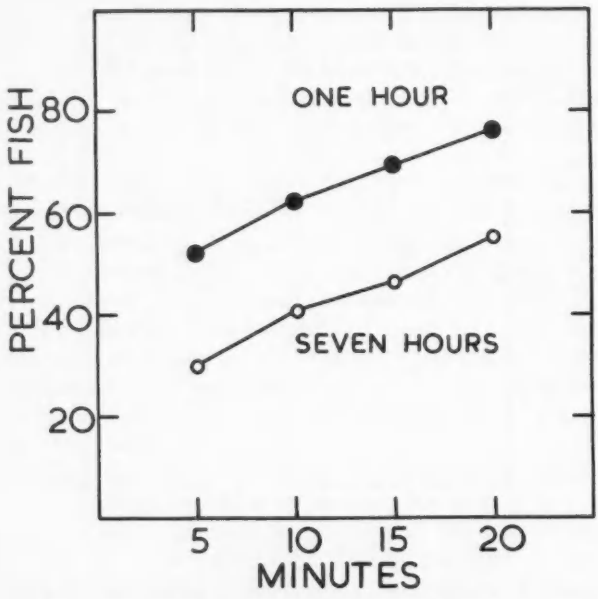

FIG. 3. Percentage of pink fry exposed in test buckets after prior isolation of schooled individuals to paper drinking cup for one hour or for seven hours; average figures for 13 tests or a total of 156 fish of each type.

Twelve groups, a total of 144 fish, were tested. At the end of five minutes, 116 fish (80.6%) were in sight above the stones. After 20 minutes this number had increased to 123 fish (85.5%). It is evident that chum fry collected from the weir screens have either previously schooled or, on emergence, lack the hiding behaviour of the unschooled pink fry. It will be shown presently that the latter seems to be the real explanation of these differing results.

In the troughs, under outdoor illumination, both coho and chums may, depending on conditions, be exposed or may remain for prolonged periods under the stones. The distribution of the coho is described in the next section. The majority of the chums are usually exposed unless startled when they quickly hide or unless the light intensity increases rapidly and is relatively high (Hoar *et al.*,

1957). The tendency to hide is also greater when the fish are in a current of running water. This may be observed in the troughs, and is discussed below; it has also been demonstrated in laboratory experiments (*Ibid.*, Table IV).

Coho and sockeye salmon smolts also hide under stones or in sheltered places. Observed differences can be readily related to the differences in intensity of schooling behaviour of the two species and the variable photoresponse discussed below.

(*b*) Occupying Territories

When a group of young coho salmon have become familiar with an environment they will distribute themselves throughout the area and remain for relatively long periods in the same general locality. If the area is small, one individual may occupy a favoured spot and, by *nipping* and *chasing*, dominate all the others and force them to remain in a relatively small part of the total area (Hoar, 1951). When the area is relatively large a more uniform distribution is common but nipping and chasing are still observed since some fish often change locations while feeding or perhaps "selecting" more favorable niches. The intensity of these aggressive activities depends on a variety of factors such as the relative numbers of fish present, their sizes, presence of food and intensity of light (Stringer and Hoar, 1955; Newman, 1956). In relatively shallow water these activities of the young coho are related to the bottom or other objects in the water although, in contrast to young trout (Newman, 1956), they do not rest directly on the bottom. In deeper water they may swim some distance from the bottom but still show a keen recognition of the objects in their environment and return for long periods to the same corner of an aquarium, the same log in a pool or the same area of stones in the stream or pond.

In the long trough described above, groups of 100 recently emerged coho fry were observed to distribute themselves relatively uniformly—occupying positions in the pools, over the stones, or among the stones so that they could be seen only as they emerged briefly to nip at another coho or to feed. The fish are not quiet. They are constantly on the move but usually travel relatively short distances—less than 30 cm.—and tend to return to the same pool or area of stones, frequently to the same spot. A similar picture is seen in many shallow pools and backwaters of the Pacific coast streams.

It should be emphasized that these societies are extremely fluid. The size of the area patrolled by an individual depends on several factors. Certain spots are occupied more continuously and held by dominant individuals through nipping and chasing; while the subordinates, or those who do not establish territories, move about more when space is not limited, although restricting their activities to a "home range" (Gerking, 1953; Newman, 1956). In any case the coho adapts readily to changes and quickly settles into a different niche when displaced.

The other three species, as juveniles, do not occupy and defend territories although at least two of them may occasionally show aggressive behaviour (Hoar, 1954), and all evidently recognize the spatial relations of their en-

vironment (Hoar, 1958). Both sockeye fry and smolts occasionally chase one another. The activity has been seen more frequently with groups of smolts. The aggressive behaviour of the juvenile sockeye is simpler than that of the coho and consists principally of chasing rather than nipping and chasing (Hoar, 1954, p. 75). Aggressive activities have occasionally been observed in chum fry but never in pink fry. This behaviour has not been seen in groups of sockeye or chum salmon in nature or in environments approaching the natural, but only in relatively restricted areas–sometimes associated with adverse temperatures. In sockeye juveniles, aggressive behaviour has been described as a displacement behaviour (Hoar, 1954). Murray Newman refers to it as "vestigial behaviour".

Finally, it should be remembered that all four species are strongly territorial and aggressive when they return to the rivers as mature adults. At that time, the pink salmon–which as a juvenile lacks aggressive behaviour–has an extremely elaborate threat display.

(*c*) Schooling

Description of schooling in four species of fry

Keenleyside (1955) defines a fish school as "an aggregation formed when one fish reacts to one or more other fish by staying near them" and adds that "the chief factor common to all schools is a definite mutual attraction between individuals". This is an adequate definition and on this basis all four species under examination may school as juveniles. The behaviour, however, varies considerably from species to species both in intensity and frequency of occurrence. Pink and sockeye fry school constantly, chums regularly and coho rarely. No two are alike in their schooling behaviour (Hoar, 1954). Pink and chum fry typically form constantly moving schools in which the individuals are similarly oriented and moving at a uniform pace, but very young sockeye fry form more stationary ("planktonic") aggregates. They may travel but often remain almost motionless, uniformly spaced but variously oriented and inactive. Again, the chum schools are less compact than the pink schools and, particularly when undisturbed for some time, individuals tend to scatter. Chum fry, however, always show some tendency to school and when one chum approaches another the mutual attraction movement is regularly evident.

Coho fry rarely school. In an earlier paper it was concluded that schooling was not one of their behaviour patterns (Hoar, 1951). The aggregations seen at that time were interpreted as chance groupings formed under the influence of such factors as current, light, temperature and cover. Typical schools are, however, readily and regularly formed in several different situations. The simplest way to demonstrate this reaction is to place some coho fry with a school of pink or chum salmon fry. The coho fry immediately show "follow-the-leader" behaviour characteristic of many schooling fish (Keenleyside, 1955). Coho smolts will show the same reaction to a school of sockeye smolts. In both cases, however, if there is adequate space the coho presently settle down to more solitary activities. More convincing demonstrations of coho fry schooling can be easily shown experimentally in the 360 cm. troughs. The following series

of observations was repeated on four different occasions with essentially the same results.

One hundred young coho fry, trapped as downstream migrants on the previous night, were counted into a bucket of water and poured from this directly into the stones of a trough with running water. The fish did not disappear into the stones but collected in groups in the pools and within three minutes commenced to swim up and down the trough from one end to the other in an orderly school. The behaviour is apparently identical to that described for the three other species as "roaming in quiet water" (Hoar, 1954, p. 77). The rate of travel by the coho was 38 to 40 metres per hour. Chum and pink fry will behave similarly in this situation, although they swim faster (55 to 60 metres per hour for chums and 45 to 55 metres per hour for pinks). Sockeye fry, on the other hand, disappear immediately among the stones and are not usually seen until the light intensity falls in the evening. The coho fry, over a period of about 30 minutes, gradually cease schooling and distribute themselves in the trough as described on page 399—feeding on surface particles, swimming among the stones and taking up positions throughout the space available to them.

In these experiments the coho were subsequently observed in the troughs for periods of one or two days and under no conditions was schooling behaviour noted. At the end of the experiment, however, the flow of water was abruptly stopped and this permitted another series of observations on the schooling of coho fry. Usually the coho were all startled by the necessary disturbance of approaching the trough to interrupt the flow of water, and hid under the rocks. When watched quietly thereafter the following sequence was regularly recorded. Within three minutes coho are rising toward the surface from the stones in considerable numbers. They collect in groups and by five minutes have started to "migrate" from end to end of the trough in an orderly manner and at a rate comparable to that given above. Chum fry and sockeye also show this behaviour when the current suddenly ceases in their environment. The sockeye come out from under the stones more slowly, but just as surely. This active schooling of coho fry continues for about 15 minutes but after 20 minutes the journeys are irregular. Individuals commence feeding, "investigate" the different niches, swim ever more frequently in and out among the stones and settle down to the stable distributions described above. By the end of half an hour the society appears much as it did before the water flow was interrupted. In comparable experiments with sockeye fry the entire group had disappeared among the stones within this time interval.

The importance of a behaviour which involves emerging and actively schooling when water currents suddenly cease or change in intensity may be considerable. It may be a mechanism preventing fish from becoming stranded when the water level suddenly falls. On the other hand, it may be a simple escape behaviour released in an animal displaced from its established niche among the stones. Orientation in running water must depend on rheotactic or "pseudo-rheotactic" response which will be disoriented when flow conditions

are suddenly altered. That the reaction is so similar when fish are introduced to a different area—whether of running or quiet water—suggests that the latter is the true explanation.

Whatever the explanation of this schooling by fish when the water flow is suddenly stopped, it is possible that this has formed the basis for the phylogenetic development of strong schooling reactions. Schooling might develop easily with these surface-feeding fish if they were displaced from a river into a lake or estuary where bottom contact is unlikely and water currents of low order. Mutual attraction between coho seems to be released by loss of contact with an established environment. In this case they react to other individuals rather than to elements of the environment. This is basically the reaction which occurs at all times in strongly schooling species such as the pink.

STABILITY OF SCHOOLING BEHAVIOUR IN SMALL GROUPS OR ISOLATED FRY

The schooling reaction may be observed with as few as two fish or even with one fish and its mirror image. However, this is basically a group reaction and is intensified as the numbers increase (p. 418). The availability of pink fry, which display a marked change in behaviour on first schooling, permitted some observations on the effect of different-sized groups on the early expression of this hiding behaviour.

Pink fry were collected during the night from the weir screens and, as before, held individually or in small groups in paper cups or paper milk boxes (capacity 1 litre). As in the other tests (p. 396), reactions were studied next morning by adding fish or groups of fish to the test buckets at 30-second intervals. In the first series of tests (repeated seven times) a group of 12 fish was compared with 12 single fish, four groups of 3 fish, and two groups of 6 fish. In the second series (likewise repeated seven times) a group of 8 pinks was compared with 8 single fish, two groups of 4 fish and four groups of 2 fish. A total of 336 fish were involved in the first series and 224 fish in the second.

Findings summarized in Figure 4 show that the interaction of even two individuals results in a different behaviour from that of single fish. On the whole, however, small groups (2, 3, 4, 6 or 8 fish) behave essentially the same as fish which have been isolated from larger schools with 75% to 85% of the individuals in sight after 20 minutes (compare Fig. 3). Reference to Figure 5, discussed below, will show that, although 6, 8 or 12 pink fry held together in a restricted area for several hours show a different behaviour from single fish, they do not display the full-intensity reaction shown by a group of fish removed directly from a large school. The five tests listed below also substantiate this conclusion. In these tests, with three exceptions all 12 fish were in sight when the last fish was added. (In two of these exceptions where 12 separate individuals were tested, and in one where a group of twelve was used, only 11 fish could be seen.)

(a) Twelve fry dipped individually from a school and added to the test bucket at 15-sec. intervals (4 replications).

(b) as in "a" at 30-sec. intervals (duplicate tests).

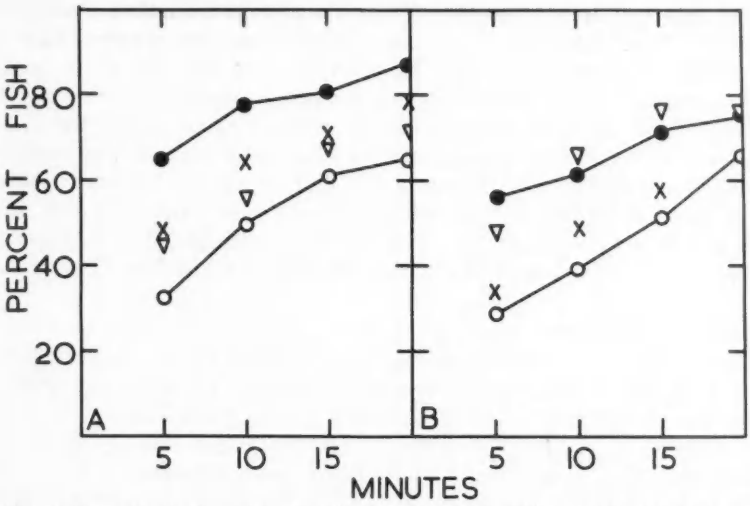

FIG. 4. Group size and number of pink fry appearing at different intervals. A. group of 12 (solid circles) compared with 12 single fish (open circles), four groups of 3 (crosses) and two groups of 6 (triangles); B. group of 8 (solid circles) compared with eight single fish (open circles), four groups of 2 (crosses) and two groups of 4 (triangles). Further description in text.

(c) individuals isolated to paper cups and after an interval of 5 to 10 minutes added to the test bucket at 30-sec. intervals in the usual manner (7 replications).

(d) three lots of four fish added as in "b" (duplicate).

(e) groups of 12 fish counted first into paper boxes and tested after 5 to 10 minutes (duplicate).

Reactions of pink salmon fry isolated from a school for several hours during the day were also investigated. In four experiments, individuals removed from a school and placed alone in a test bucket did not disappear beneath the stones in a period of two hours. This indicates that individuals separated from their school during the day may not hide under stones. However, the stability of this negative hiding behaviour was tested more rigorously by isolating individuals to paper drinking cups for one or seven hours before testing their hiding responses. In this case, the fry were not only removed from the school but from the natural bottom environment of stones. The findings have already been referred to in Figure 3. The tendency to hide increases with longer periods of isolation. About 24% of those isolated for one hour remained hidden after 20 minutes test, while 45% of those isolated for seven hours were still under cover at a comparable time.

(D) FEEDING

Young Pacific salmon are basically dependent on their eyes for the location and capture of food. All of the four species studied will dart rapidly to the

surface and snap at particles of food. At the time of migration, however, the reaction is more frequently observed with the coho and sockeye than it is with groups of pink and chum fry. Coho fry, in particular, frequently "sample" surface particles, while chum and pink fry are constantly on the move, and the sockeye are hiding in dark places. The sockeye smolts during the evening and the coho fry during the day often swim (jump) out of the water and capture insects flying near the surface. Older chum fry, captured near the end of their downstream migration, are observed to feed more and school less regularly when undisturbed in quiet water. All species can be readily conditioned to take a variety of foods at different places and in different ways.

(E) Escaping Predators

The response to a predator—which is also released by the sudden approach of any large object—is a rapid change in the direction of swimming. This may or may not be oriented to cover, depending on the species of fish as well as the availability of suitable hiding places. The movements are too quick to be precisely described from general observations. Such differences as are noted appear to be related to the length of the fish. Detailed analysis from motion pictures might show species differences. If pursued when cover is not available, single animals make a series of short darting movements in different directions which may or may not form a sinuous, snake-like trail. The behaviour of groups of fry, in contrast to isolated individuals, shows marked species differences. This will be illustrated with two experiments.

In the first set of experiments the reactions were compared in buckets of water arranged as described above with a layer of stones on the bottom. They were placed out of doors. The fish tested had been captured during their migration the previous evening.

Ten fish of any one species were added in a group to a bucket, and the number of individuals appearing above the stones was recorded at one-minute intervals for 10 minutes (usually a stable situation). The fish were then startled by waving the hand and tapping the bucket until a maximum number (frequently all) disappeared beneath the stones. Numbers appearing at minute intervals were recorded for 5 minutes, and the fish then startled as before. Pink, chum and coho fry were always tested at the same time. Sockeye—which emerged somewhat later —were examined later but under similar conditions. Quantitative data based on three such experiments are given in Figure 5.

Differences in the behaviour of the four species are obvious. Groups of pink salmon, when alarmed, do not hide under stones but scatter wildly in different directions, losing their orderly arrangement and darting to and fro. A few can be driven under cover but this is not their typical group reaction when alarmed. Coho, chum and sockeye fry, on the other hand, disappear beneath the cover of stones. As previously described, the sockeye fry usually emerge only at low light intensity. In fact, when the buckets were emptied and the stones removed one by one, the ten sockeye fry were regularly found under the last stone. In the initial period of the test, chums emerge rather quickly; coho more slowly. When

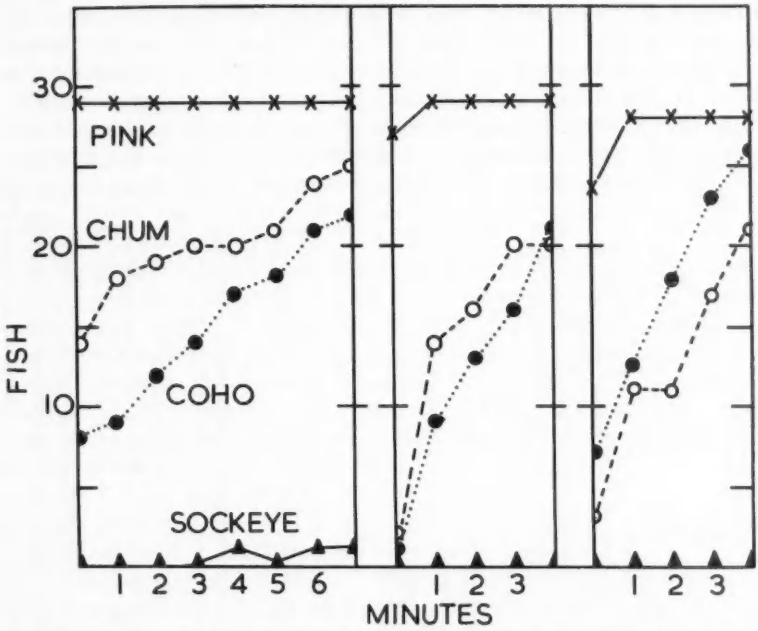

FIG. 5. Numbers of salmon fry not hiding under stones on the bottom of a bucket. Maximum response, 30 fish; left series, immediately after adding to the bucket; middle and right series, each after startling the fish; further description, text page 404.

the fry are repeatedly startled the coho show less and less marked responses to the standard stimulus and, by the third occasion, fail to go beneath the stones. The response of the chums remains much the same in successive tests.

General observation confirms the reality of this difference in the responses of coho and chum salmon fry depicted in Figure 5. The failure of the coho to show a cover reaction when repeatedly startled by a stimulus of this type is a simple form of learning described as "habituation" by Thorpe (1956). It is of obvious value to an animal living in shallow water, where it must frequently encounter passing shadows and similar disturbances. Differences in rates of adaptation of coho and chum salmon fry to turbulent water (MacKinnon and Hoar, 1953) and to light (Hoar *et al.*, 1957) have also been described. In each case, coho after a time failed to respond to changes in stimulus while the reaction remained at high level in the chum fry.

The second series of experiments demonstrates the relative values of these different reactions to young salmon living in shallow exposed streams. Four groups of 100 fry of each species were placed, on different occasions, in the long troughs of running water which provided alternating pools and areas of gravel. Fish were left in these troughs for 24 hours (occasionally longer) before the stones were removed and counts made of the number of fish remaining in

them. Pinks and chums were always studied at the same time in a pair of troughs placed side by side with the groups alternated from one piece of apparatus to the other in successive tests. The coho and sockeye tests were carried out together following the pink and chum experiments.

The results, shown graphically in Figure 6, were produced by a co-operative group of crows (*Corvus*), which quickly spotted the relatively exposed pink fry and exploited a behaviour pattern which appears to be inadequate

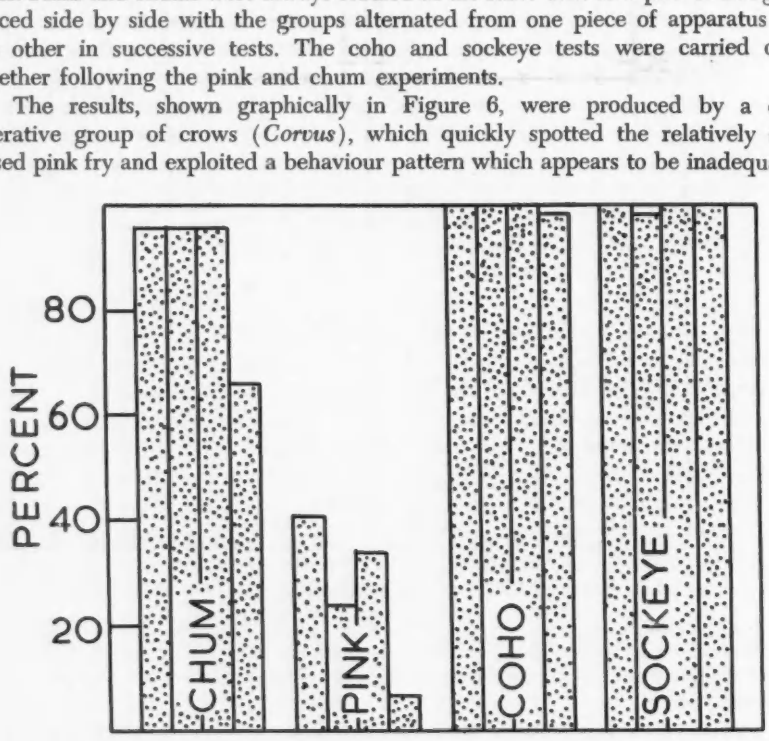

FIG. 6. Predation by crows; expressed as percentage of fish remaining in trough after 24 hours (first test with pinks and chums, 48 hr.). Tests carried out in order from left to right, with chum and pink groups tested simultaneously first, and coho and sockeye fry together directly after.

for survival in shallow exposed environments. The crows were observed to visit the area of the experiments frequently when men were not in the vicinity; bird faeces were found in the troughs and injured pink salmon or a head or tail of a pink salmon found each time the troughs were emptied. The advantages of the hiding behaviour and the disadvantages of the strong schooling behaviour are obvious with these small salmon in shallow water. The rapid exodus of the pink salmon from the rivers to the ocean is vital to their survival. In a stream such as Hooknose Creek, where these experiments were performed, the pink salmon migrate first and most rapidly to the ocean each spring.

THE DIRECTING OR ORIENTING FACTORS

The behaviour patterns just described are expressed as a series of stereotyped muscular movements. The orienting mechanisms to be discussed in this section are less rigid, permit differences in intensity of action and often de-

termine where the fixed movements will be performed. They form the basis of the animal's adaptability and introduce a complexity and diversity into behaviour which would otherwise be a rigid pattern of movements. Several factors with potential orienting action may play on the animal at the same time. Like any stimulus-response situation the activity expressed in such cases depends on the relative intensity as well as the nature of the combined stimulating agents. For example, high temperature may alter the responses of fish to light (Andrews, 1946) and reactions to current may be markedly changed by both light and temperature.

The term "taxis" is sometimes used for the type of orienting mechanism discussed here. It does not, however, seem entirely appropriate to any of the responses of these juvenile Pacific salmon. The reactions are rarely of the all-or-none type and lack the fixed character of the classical "forced movement" or taxis. The terms "directive factors" (Fry, 1947), "orienting factors" or "steering mechanisms" (Baerends, 1957) are preferred. In this category, light, temperature, current, salinity and the geography of the environment will now be considered.

(A) Light

Light modifies the behaviour of the juvenile Pacific salmon in three different ways. The seasonal cycle of changing length of days induces physiological (photoperiodic) changes which are probably responsible for the "internal motivation" associated with migration of the smolts (from unpublished data). The diurnal sequence of varying light intensity imposes a basic rhythm on all the activities of these fish. The different photosensitivity of the various species and the changes in photosensitivity which occur in each species during its development and growth are responsible for some of the most interesting differences to be found in the migratory activities of the juveniles. Seasonal changes will be mentioned later. In this section the diurnal rhythm and the species differences are considered.

DIURNAL RHYTHM IN ACTIVITY

A diurnal rhythm can be demonstrated in almost any of the activities of the young salmon. The pattern, however, varies with the species of fish and the activity under examination. In one case activity may be high at midday and low in the middle of the night, while the reverse may be true in another instance. For example, sockeye fry, which in general avoid bright light, show a midday low in the rate of swimming in quiet water (Fig. 7); sockeye smolts, likewise photonegative in reaction, are stimulated more at midday when in exposed locations to swim upstream against the current (Fig. 8)—perhaps an appetitive behaviour associated with avoidance of bright light; coho fry settle to the bottom of a tank in the evening and show a decline in the rate of nipping at lower light intensities (Fig. 9); chum and pink fry swim faster and school more intensely in the morning and evening (Hoar, 1956, and section "C" below). Such differences have been repeatedly recorded during this investigation.

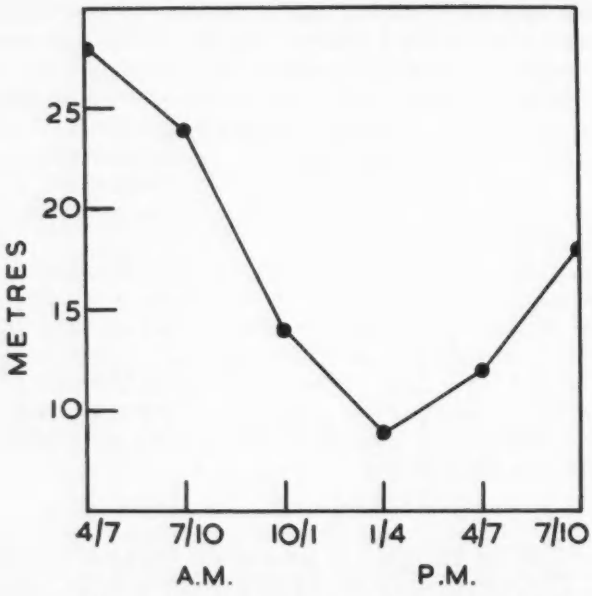

FIG. 7. Diurnal rhythm in the activity of sockeye salmon fry expressed as metres travelled by schools of 20 individuals in circular channels 251 cm. in circumference (Hoar, 1956). Each point is a mean value for 20 to 35 ten-minute observation periods.

Similar observations may be made under natural conditions. Some of the most convincing demonstrations were seen in a miniature river system about 15 metres long where the activities could be followed for many days. Water flowed into a narrower inlet portion (3 m. long) through a leakage in a dam. Fish could not escape in this direction. The channel widened rapidly from this inlet stream into the major portion of the system (length about 12 m.). This varied in width from 1.5 m. at the upper end to 4 m. at the lower end where the water flowed over a low dam. The depth, for the most part, was about 10 to 20 cm. but two deep holes were provided in the central part of the wide area of the channel by barrels (50 cm. diameter and 70 cm. deep) sunk into the ground so that their tops were well beneath the surface of the water.

Sockeye smolts placed in the miniature river system gradually disappear in the barrels as they encounter them in their leisurely journeys. During the day, individuals not infrequently emerge from the barrels but usually remain near them and move about slowly or not at all. In the evening, however, the picture changes rapidly. As the light intensity falls from 500 to 150 foot-candles, and more particularly around 100 ft.-c., the smolts emerge from the barrels and become more and more active. Below 15 ft.-c. they are extremely active, swimming rapidly many places throughout the pond. They show intense feeding behaviour from about 50 ft.-c. to intensities where observation is no longer possible (4 to 5 ft.-c.),

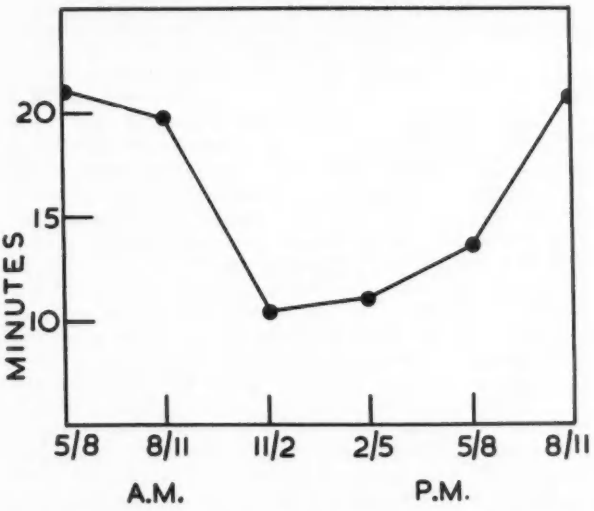

FIG. 8. Diurnal rhythm in activity of sockeye smolts, as minutes elapsing before 50% of a sample of 10 fish jumped from a downstream pool into an upstream pool over a 2.5-cm. waterfall created by a vertical plywood dam in the 360-cm. trough. Each point is the mean value for 10 groups of fish; flow 25 to 35 litres/min.

jumping from the water for insects. With a group of 50 smolts the pond seems to be alive at light intensities below 5 ft.-c. In the dim twilight forms can be seen darting to and fro, jumping out of the water for insects, and swimming rapidly in many directions.

Sockeye fry placed in troughs arranged with pools and areas of stones to provide shelter show a comparable behaviour. Groups of 100 fry placed in these troughs disappear among the stones and are rarely seen during the day. In the late evening, however, when the light intensity falls below 50 ft.-c. (more often below 10 ft.-c.) they emerge in large numbers and swim to and fro in schools from one end of the trough to the other.

The increased activity seen during the evening in all actively migrating species is fundamental to the mechanism of their migration. The declining activity in coho fry must, at least in part, be responsible for their continued residence in fresh water.

VARIABLE PHOTOSENSITIVITY

The variable photosensitivity of the juvenile Pacific salmon has been especially considered in three previous papers (Hoar, MacKinnon and Redlich, 1952; Hoar, 1955; and Hoar *et al.*, 1957). The reactions depend both on the absolute intensity of the light and on the rate at which it changes. All species show a tendency to avoid extremely intense illumination but some species will show this avoidance only when they are suddenly brought from dim to bright

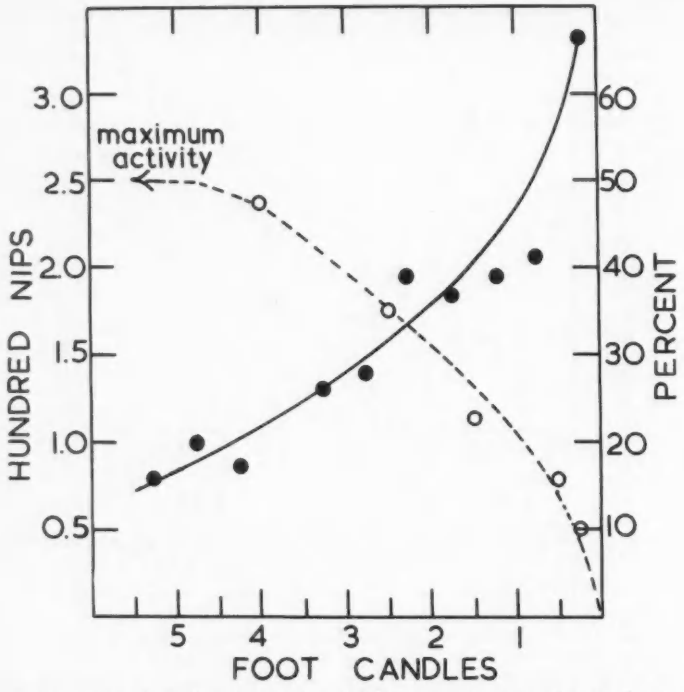

FIG. 9. Diurnal rhythm in activity. Solid line, percentage of coho fry in lower third area of a 90-cm.-high tank (Hoar, 1954, p. 83) under decreasing intensity of natural light; records were made at five minute intervals for 1.5-hr. periods with 6 groups of 12 fish, 18 hours (total) of observation. Broken line, number of nips by groups of 12 trout fry (*Salmo gairdneri*) in a 180-cm. long aquarium (Hoar, 1951, p. 243) under artificial light at intensities indicated when changed every 15 min., with 10-min. observation periods after 5 min. adaptation; total of 18 hr. observation. All light measurements with "Photovolt Universal Photometer" (Model 200). Data collected by G. E. Stringer.

light. The physiology of the eye and related photosensitive areas of the brain (Hoar, 1955) has not been adequately studied but it may be assumed that interesting differences will be found in these mechanisms of the four species.

Following is a list of the pertinent associations which have been experimentally demonstrated in previous studies.

1. The sockeye salmon, both as fry and smolts, are photonegative. In tests where the environment resembles a natural one (long troughs with stones or miniature river system) they always avoid light more strongly than other species at a comparable stage in development. Laboratory tests frequently show similar comparative differences.

2. Recently emerged sockeye avoid light more actively than older (one or two month) fish. The data suggest that the light intensity for optimum activity and the preferred illumination increases—at least for a time—as the fish grow but never reaches the level found in the other species.

3. Coho fry are active and apparently undisturbed by a wide range of light intensities. They habituate (Thorpe, 1956) readily to changing intensity and are often characterized by an apparent indifference to the prevailing intensity. This is associated with a life in shallow streams where conditions of light and shade often change. The ready habituation of coho to repeated stimulation of any particular type has been mentioned.

4. At night coho fry may be active at very low intensities of illumination but do not show the marked nocturnal increase in activity which characterizes the other three species. They move into shallow water, settle somewhat, cease feeding and nipping.

5. Coho smolts retreat to deeper water and remain in darker places than do coho fry.

6. Chum fry, following their initial emergence from the gravel, prefer bright light and more than 50% of them may be expected in exposed locations although they will retreat to deeper less intensely illuminated areas when the light rises to 500 or 1000 ft.-c. When schools of chum fry were placed in the miniature river system described above, large numbers of them could be observed at all light intensities during the day. Some remained in quiet groups along the edges of the pool while others swam persistently into the headwaters of the inflow stream. Contrary to earlier conclusions based on laboratory experiments, they did not always remain in the fastest water (MacKinnon and Hoar, 1954).

7. The photoresponses of the pink fry are similar to those of the chum although the recently emerged schools fail to hide and are more responsive to changing light intensities. As the light intensity increases the very young fry retreat to deeper water if this is possible and show a sharp surfacing reaction at very low intensities. This surfacing reaction of the recently emerged pink salmon fry (either schooled or non-schooled) is associated with intense swimming in the surface layers of water at low light intensities. It is considered a basic mechanism in the rapid downstream migration of this species. It disappears several weeks after emergence from the gravel (Fig. 10).

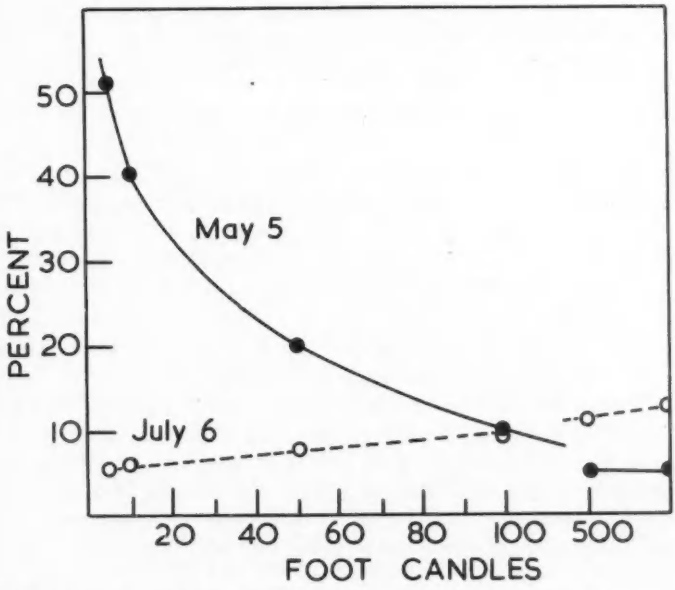

FIG. 10. Percentage of pink salmon fry in the upper third portion of a 180-cm.-deep tank in relation to changing light intensity. Redrawn from Hoar *et al.*, 1957, fig. 3.

Photoresponses of the alevins have not yet been studied and there is little information on the behaviour of Pacific salmon prior to the free-swimming stage. Woodhead (1957) has measured the activity of salmon (*Salmo salar*) and trout (*S. trutta* and *S. irideus*) larvae in relation to light intensity and age. The recently hatched larvae are photonegative and show increasing amounts of movement as the light intensity is raised above 0.005 metre-candle. Over a limited range the duration of activity is directly proportional to the logarithm of the light intensity. As the larvae grow there is an increase in the level of activity at all light intensities until finally they are continuously active throughout the observation period. At this point the behaviour of the young fish changes, negative phototaxis is lost and feeding commences. Comparable data, when developed for young Pacific salmon, should clarify many of the details of emergence from the gravel and initiation of migration.

(B) TEMPERATURE

Temperature is an important factor in considerations of the biology of any cold-blooded animal. The rate of development and time of emergence of young salmon is strictly dependent upon the temperatures during development. Although the timing of migration is thus at least partially controlled by temperature, this factor does not appear to play a vital part as one of the steering mechanisms of the various behaviour patterns. In many places the mass exodus of young salmon from the streams occurs while the water temperatures are still relatively low and showing small variations from day to day. Temperature may, however, be important in two ways so far as those fish are concerned which remain in the streams when the days become warmer and water temperatures rise sharply.

Keenleyside and Hoar (1954) found that, in experimental situations where young salmon are induced to swim actively against a current, a sharp rise in temperature of 4 or 5°C. will regularly induce a change in direction producing active negative rheotaxis, in chum and coho salmon fry, although the reactions are not changed in sockeye fry. Active swimming with the current when temperatures rise sharply is considered a mechanism which hastens or induces downstream movement in chum salmon which have remained past the time of the peak migration of the species. The significance of the different response apparent with the sockeye is not understood but the observations are believed to be valid. This may form the basis of a behaviour which in some places results in mass upstream movements of sockeye underyearlings. Sockeye which are somewhat larger than recently emerged fry become less sensitive to light and, retaining their strong positive rheotaxis, may be stimulated by rising temperatures to swim more strongly against the current. The reaction might be caused by the direct acceleration of metabolic processes, or temperature might be acting as a directing factor associated with rheotaxis as in the case of the chums.

(C) CURRENT

An animal whose habitat is flowing water must often orient its activities with respect to water currents. In this investigation juvenile salmon have been

observed to hold position in the current, to swim actively against the current, to swim actively and vigorously with the current or to express their varied behaviour patterns with apparent disregard for this factor. Many attempts have been made to demonstrate the general principles which must be operating as directive agencies of behaviour in flowing water. Details have been recorded on the basis of comparisons made in a rotating system of currents (Hoar, 1951), in laminar and turbulent flow, in miniature waterfalls and miniature river systems (MacKinnon and Hoar, 1953; Hoar, 1954). The following responses are characteristic and pertinent to an understanding of the ethology of the species.

1. When it is possible to see objects in the environment, all species and stages respond to a sudden change in current velocity by swimming vigorously against the current and, if the velocity is not too great, by holding position.

2. An optimum current for a maximum response can be readily demonstrated experimentally if responses are compared at a series of current velocities.

3. Under strictly comparable conditions chum fry respond more strongly to current than coho, pink or sockeye fry of the same age. The sockeye smolts respond more vigorously than the coho smolts.

4. Juvenile coho smolts or fry show an habituation (Thorpe, 1956) to stimulation by constant water currents which is not marked with chum fry or sockeye fry and smolts. Pink fry have not been adequately studied. Although the coho respond sharply to sudden changes in velocity they soon become indifferent to continuous currents and cease to orient strongly with respect to them.

5. Fish which are suddenly displaced or lose contact with their normal environment may swim rapidly with the current, or school about showing an indifference to it.

Species differences in the reaction to water currents were also demonstrated in some experiments carried out at Port John in 1955. In these tests the four species of recently emerged fry were compared at the same time in identical pieces of apparatus. The apparatus selected for these experiments (Hoar, 1954, p. 89) had been used to compare the reactions of coho and sockeye smolts and had given reasonably consistent results. Four of these 225 cm. long troughs were placed side by side under a shelter where they could be observed in diffuse light (50 ft.-c. or less) without startling the fish. The troughs were divided for half their length by longitudinal vertical plywood partitions. Water (6–8 litres/min.) flowed into the closed end of one of these channels and stimulated the fish to swim against the current. The flow of water was alternated from channel to channel in successive tests.

Groups of 20 migrants fry were placed in the troughs at midnight; observations were commenced at 6 a.m. the following morning and repeated at about two-hour intervals for seven times during the day. The four kinds of fry were assigned to the different troughs by random numbers. There was no flow of water in the troughs during the night nor between the different tests during the day. Distribution was recorded as the number of fish counted in each channel at the moment of observation and counts were made at precisely one-minute intervals for six times: before starting the flow of water, when the flow had been maintained for 10 minutes, and after the flow had been on for 30 minutes. Thus, six counts were made three times for each observation and observations were repeated seven times for each group of fish.

Data summarized in Figure 11 show the comparative responses based on seven such experiments (May 1 to May 14). The numbers on the bars give the ratio of the number of fish in the channel with flowing water to the number in the channel with no flow. Several differences in behaviour are emphasized in this graph. In the first place, the ratios at the initial recording show a contrast between the chum and coho on the one hand and the sockeye and pink on the other. With pink and sockeye fry, distribution between the two channels in the "no flow" situation is equal but at this time there are many more coho

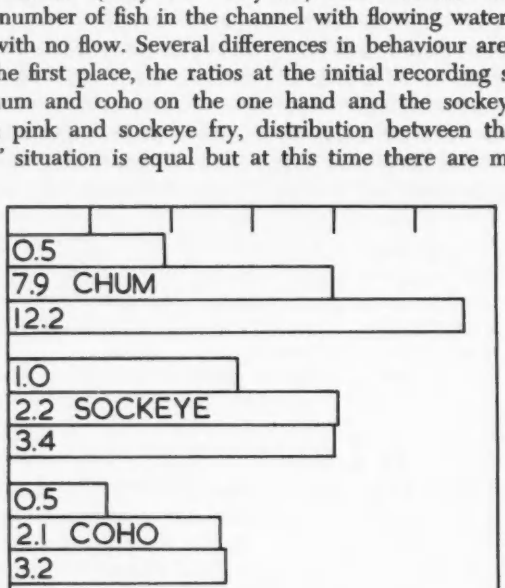

FIG. 11. Responses of salmon fry to flowing water. The three histogram bars in each series are, from top to bottom, the number of fish counted in the "flow channel" before the flow was commenced, after 10 minutes, and after 30 minutes of flow; numbers on the bars are ratios of fry in "flow channel" to fry in "no-flow channel".

and chum salmon in the "no flow" side of the system. It will be recalled that this is the channel to which the fish, in the previous test, had been attracted by the current. The recognition of and preference for a territory to which these species have previously been drawn is strong. Houston (1957) noted it and discussed the various possibilities in his salinity preference study. In the second place the reactions of the chum and sockeye to current are of a much higher order than those of the coho and pink fry. Differences between the chum and coho have been discussed and analyzed (MacKinnon and Hoar, 1953). The relative responses of sockeye in the smolt stage are strong and it is probable

that those of the fry appear somewhat less than the chum in this test only because of the smaller size of the fish (Fig. 1): the 10-minute record is essentially the same in both. The responses of the pink fry, on the other hand, are of quite a different order from those of the other schooling fry. This finding was not immediately accepted, and two additional experiments were performed in which the responses of pink and chum fry of comparable size and age were rigorously compared. One test, involving three days' observations with flows of 7–8 litres/min. gave a five times greater response for the chums after 30 minutes. The other test, involving two days observation and flow of 4–5 litres/min. showed twice as great a response on the part of the chums. Thus, in this response as in several others the pinks are distinct among the other strongly schooling species.

TABLE I. Diurnal variations in the response of salmon fry to water currents. Description in text, below.

	Percentage in current		
Species	6 a.m.	Noon	6–8 p.m.
Chum	70.0(66.1)	51.7(48.2)	43.4(36.6)
Pink	60.3(59.5)	10.2(2.7)	32.1(32.0)
Sockeye	58.4(48.3)	28.8(3.4)	35.1(24.1)
Coho	60.3(56.5)	25.1(20.1)	21.9(15.0)

The data obtained in the major experiment of this group were also examined for diurnal variations in the intensity of response to current. The findings are summarized in Table I. Two series of values are given. The unbracketed numbers are percentages of the total numbers of fish involved in the test which were recorded in the channel of flowing water at the six intervals of both the 10 min. record and 30 min. record. Seven different groups of 20 fish were involved, making a total possible count of 1680 ($7 \times 20 \times 2 \times 6$). The bracketed percentages were calculated similarly after subtracting the number of fish in the "no flow" channel from the number in the channel of flowing water. Such a procedure seemed reasonable to the writer since all the fry are very active, never remain long in one place, and in certain cases obviously avoid the current by moving into the channel of quiet water. This was most marked with some groups of sockeye and pinks at midday.

On the whole the data are consistent with the behaviour which has already been described for the four species of fry. The diurnal rhythm is most marked in the activities of the recently emerged pink and sockeye fry. Chums respond most consistenly and strongly to current at all times of the day. When morning and evening values are compared the coho fry shows the greatest depression in activity. All groups may be showing a measure of habituation to the conditions of the experiment by the time of the evening readings. On the other hand, it seems more likely that the relatively low evening values are related to the tendencies of three species to lose position or migrate at this time of the day and of the third (coho) to show reduced activity. The light intensity in the shack was one foot-candle or less at the time of this evening reading.

(D) Salinity

Houston (1957) has studied the responses of pink, chum and coho juveniles to sharp salinity gradients. Pink and chum salmon fry and coho smolts make a sharp response to either isotonic or hypertonic sea water. Coho fry, on the other hand, although responding to isotonic sea water show an avoidance of hypertonic solutions. In other words, prior to the smolt transformation the coho avoid strong sea water; after the transformation they prefer sea water to fresh water.

Salinity gradients cannot be directing factors in the downstream migration of juvenile salmon but may have significance in the orienting of the juveniles in estuaries and toward the more saline offshore waters. They may also orient the fish if it experiences strong positive rheotactic stimulation from rivers flowing into the sea, and thus prevent a return to fresh water at this time.

Salinity is listed here for two reasons. In the first place, a preference for saline waters is associated with an ability to live and grow in hypertonic salt solutions. Coho salmon fry, like many of the juvenile salmonids, cannot survive in hypertonic sea water (Black, 1951) until the smolt transformation. The acquisition of this ability in the fry stages of some of the species of *Oncorhynchus* has been an important factor in the evolution of their early sea going behaviour. In the second place, it may be that the behaviour of actively preferring sea water should be catalogued among the consummatory acts (Baerends, 1957) of the salmon's behaviour and that much of the activity of migration is appetitive behaviour leading to swimming in saline waters. Movement into sea water as juveniles and into fresh water as mature adults "appears to satisfy" a basic physiological requirement, but until more is known of this behaviour and the associated physiology it must be classified with considerable reservation.

(E) Objects in the Environment

All the young salmon learn quickly to recognize various features of the area in which they live. Young coho occupy and defend an area of an aquarium or trough or return persistently to the shelter of one particular stone. The schooling species will swim back and forth in only one channel of a maze of channels although "exploring" from time to time the entire pattern of channels (Hoar, 1958). The schooling species may also show perference for one end of a trough and make regular "exploratory" journeys to the other end of the trough, travelling from the preferred area very slowly and returning to it rapidly (Hoar, 1954, p. 77). The strong preference which chum fry show for the compartment of a trough to which they were previously drawn by current or salinity has been mentioned. All these activities show a keen recognition of objects in the environment, an apprehension of spatial relations, and an ability to orient behaviour accordingly.

The behaviour sometimes described as "following along the shore" is an oriented behaviour which the schooling species may show with respect to the wall of their experimental apparatus. These contact reactions have been measured and likened to thigmotaxis (Hoar, 1954, p. 74). No particular significance

is ascribed to such reactions in the discussion of phylogeny but the importance may be considerable in the orientation of schools of fish in large bodies of water. The more marked tendency of coho to remain near solid objects is associated with their life in pools and among stones.

When hiding, individual chum fry have been observed to become relatively unresponsive and motionless as they press into close contact between stones. Occasionally the head and eyes of an individual can be seen while most of the body is in close contact with the stones. Such fish are not easily startled and may remain quiet even though touched lightly with a pencil. Such behaviour may be characteristic of young salmon and important to them but it has not been studied in aquaria where it might be properly observed.

THE APPETITIVE BEHAVIOUR

These, then are the basic behaviour patterns of the four species of young Pacific salmon in fresh water. The fish respond in characteristic ways to cover, to the geography of their environment, to food, to predators and to other small fish. The different movements are oriented with respect to environmental gradients of light, temperature, current and salinity as well as to specific objects such as food, shelter or other animals.

This framework, however, does not include a large part of the activity of these fish. When placed in a long trough, pink, chum and sockeye fry will swim to and fro in orderly schools almost constantly for days (Hoar, 1954); in circular channels they will travel regularly in one direction for equally long periods of time (Hoar, 1956, 1958); in a tall narrow aquarium sockeye smolts will swim rapidly up and down as individuals (Hoar *et al.*, 1957); groups of coho swim to and fro when first placed in confinement but later spend much time "exploring" various parts of the space available to them. In earlier papers these activities were variously labelled as "roaming in quiet water", "escape behaviour" or "exploratory behaviour". The escape from confinement may be as distinct a behaviour pattern as the escape from predators but, at the present time, all these activities seem to fit into the concept of "appetitive behaviour". If the sockeye smolts confined in the tall aquarium are released into a pond or large tank they form a relatively quiet or slowly swimming school. The "exploratory behaviour" of the coho results in feeding or occupying territories. The "roaming in quiet water" by the schooling fry is a constant series of schooling reactions to other members of the group.

Appetitive behaviour ("searching behaviour by which the animal finds the corresponding releasing or satisfying situation"—Baerends, 1957, p. 248) is thus associated with the five different behaviour patterns and also with the directing factors. This concept is fully in line with current ethological theory (*loc. sit.*). In the present analysis, migration itself has not been listed as a distinct behaviour pattern. There may be a migration "super-instinct" (Baerends, 1957, p. 246) which would be the goal of much of the general locomotor activity observed in young migrant salmon. However, until more is known of the ethology and physiology of juvenile salmon it seems preferable to follow the simplest classification possible.

The almost constant swimming activity of the schooling species in quiet water has been examined in considerable detail (Hoar, 1956, 1958). One important point for the present discussion is that its speed and constancy of direction are in part dependent upon the size of the group. Although single individuals (chum or pink fry) may swim steadily in a constant direction for prolonged periods the speed is greater with groups of optimum size. This was analyzed carefully with schools of pink salmon fry.

Different numbers of pink salmon were observed in circular channels, 314 cm. circumference (Hoar, 1956), under outdoor illumination. Groups of 10, 20 and 40 fish were compared at the same time in one series of tests and groups of 25, 50 and 100 fish compared in another. In each case the fry were placed in the channels at about 9 a.m. and watched for 10-minute periods at approximately two-hour intervals thereafter for six times during the day (60 minutes of observation per group). The experiment was repeated three times with each different size group, making a total of 18 observation periods or three hours in each case. The number of circuits completed by the school (75% or more of the individuals) was recorded as well as reversals of direction or other irregularities.

Findings reported more fully elsewhere (Hoar, 1958), are summarized in Figure 12. The distance travelled as well as the constancy of direction is greater in larger than in smaller schools. The optimum size for a school of salmon fry will probably vary with the size of the area in which they are swimming as well as other factors. In the circular channels used in these tests schools of 50 travelled about as fast as schools of 100 fish. In these relatively narrow and circular channels it was evident that the group of 100 individuals sometimes broke up into several well organized groups and that delays resulted when these groups encountered one another. In a larger, differently shaped area, this might not occur. The principle demonstrated seems to be that the active orderly swimming of the school is a group reaction and that small numbers or isolated groups of pink and chum salmon fry will not behave in as orderly and precise a manner as the larger schools.

THE INTERNAL MOTIVATION

Some kinds of behaviour are more likely to be observed at one time than at another. Salmon feed as juveniles and reproduce only at the end of their life cycle; they migrate seaward in the spring and leave the ocean when sexually maturing. Students of behaviour use the term "internal motivation" to describe this "state of the animal responsible for its readiness to perform the behaviour pattern of one instinct in preference to all other behaviour patterns" (Thorpe, 1951). Its physiological basis is in no case well understood but its existence is evident and it cannot be denied that many activities are likely to occur only at certain stages in the development of the animal.

Seaward migration of the Pacific salmon occurs during a relatively short period of the year. It is possible that the physical conditions and directing factors are present only during this period and that the migration is purely

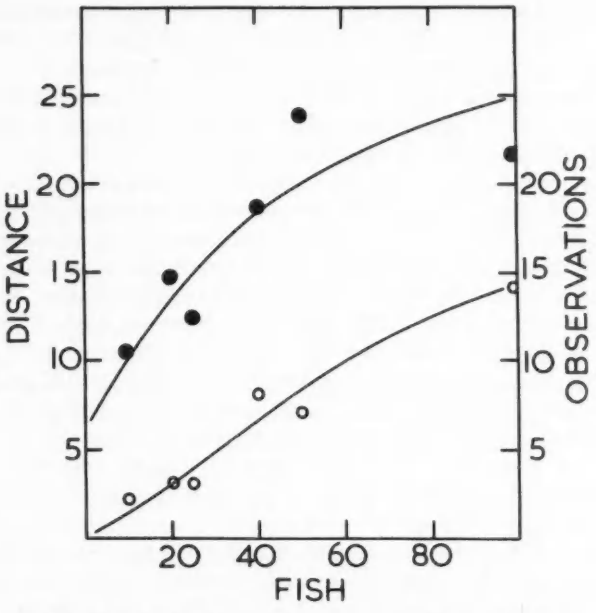

FIG. 12. Schooling by pink salmon groups of different size. Upper graph, distance measured in number of 314-cm. circuits completed per 18 minutes during 3 hours of observation; lower graph, number of observation periods during which circling was uninterrupted (possible maximum, 18).

fortuitous. Three factors, however, argue against such an extreme view. In the first place, coho although they may move downstream as fry (Hoar, 1954) do not make a mass exodus to the ocean until they become smolts and this transformation is known to involve biochemical changes with the significant development of resistance to sea water (Hoar, 1953). The sequence argues strongly for the development of a physiology which favours the behaviour of migration. In the second place, it is evident that there has been a biochemical evolution in the Pacific salmon which permits progressively earlier survival in sea water. Coho fry are killed by sea water and do not acclimatize to it (Black, 1951). Chum and pink salmon enter sea water as fry and do not require any smolt transformation. The speculation seems justified that there has been an evolution in an earlier development of the internal motivation associated with seaward migration and that the climax is seen in the pink salmon which migrates earliest seaward and begins its life as a silvery pelagic animal (Fig. 1). In the third place, the behaviour of these migrant fish does change over a period and several activities associated with migration are altered when the fish are retained in fresh water. One of the most striking of these is the change in photo-responses which have already been described in pink and sockeye fry (see also Hoar, 1956, Fig. 7).

Another is the observation that chum fry captured at the end of the migration period and observed in troughs and circular channels spend more time picking particles from the surface of the water (feeding behaviour) than in straightforward swimming and that they swim less persistently forward in a winding channel (Hoar, 1958). The theory that internal motivation is important to seaward migration can at least be seriously considered.

The physiological basis for this hypothetical motivation is unknown. An activation of the thyroid gland of seaward migrating salmonids in the smolt stage was first described by the writer in 1939. This finding has been confirmed several times and, experimentally, thyroid treatment has been shown to induce guanine deposition in the skin and growth changes similar to those of the smolt transformation (Hoar, 1957). Baggerman's recent work (1956 and unpublished) indicates that this hormone will also alter salinity preferences. Some unpublished experiments, carried out in 1949, did not, however, show a significantly increased salinity resistance in coho fry treated 48 to 96 hours with synthetic thyroxine. The data indicated that the assumption of a marine habitat involves more than a change in the level of thyroid hormone. A similar conclusion has been reached by other workers using different species of fish (Hoar, 1957).

The effect of thyroid hormone in stimulating locomotor activity of fish may be important in the development of an internal environment appropriate to migration (Hoar, Keenleyside and Goodall, 1955). The increased responsiveness and activity of coho and Atlantic salmon in the smolt stage has been noted (Hoar, 1953) and might be the direct effect of the increased thyroid activity described.

The thyroid gland, however, is only one unit in a complex system for chemical regulation. Hormones of the pituitary have been associated with salinity resistance and osmoregulation in teleosts. The literature has been reviewed by Hoar (1957) and by Pickford and Atz (1957). Changes in pituitary activity occur seasonally and can be induced by a control of the photoperiod in Pacific salmon, as in many other animals (Hoar, 1957; Newman and Hoar, 1957). At the moment, however, it seems unwise to go farther than to emphasize the likelihood of an endocrine basis for this internal state of readiness which makes seaward migration more likely in the spring. Some evolution in these mechanisms must have permitted the progressive abbreviation of the freshwater life and lead to the condition of obligatory seaward migration.

DISCUSSION

Evolutionary Changes in Behaviour

Pertinent differences in juvenile behaviour are listed in Table II and an attempt made to compare their relative intensity in the four species. All species differ in one or more characteristics. Only the chum fails to show an extreme in one direction or another. The river life with its associated territorial behaviour and low nocturnal activity is characteristic only of the coho juvenile; a pelagic lake life with smolt metamorphosis characterizes the sockeye; a pelagic ocean life

TABLE II. Comparison of the activities of juvenile salmon fry or underyearlings. Intensity of activity rated according to number of + marks; 0 indicates that this activity has not been seen in that species.

	COHO	SOCKEYE	CHUM	PINK
River residents	+	0	0	0
Lake residents	+	++	0	0
Fry prefer sea water	0	+	++	++
Fry hide under stones	+++	+++	++	+
Nipping behaviour	+++	++	+	0
Territorial behaviour	++	+	0	0
Schooling behaviour	+	+++	++	++++
Smolt transformation	+	+	0	0
Increased activity at night	0	+	+	+
Swim into surface film in darkness	0	0	0	+
Positive rheotaxis	+	++	++	+

with early loss of reactions to river bottom after emergence and a failure to develop the cryptic coloration present in bottom dwelling fish are unique characters of the young pink salmon. The chum displays intermediate characteristics between the coho and the pink type.

Tchernavin's (1939) arguments for a freshwater origin of the Salmonidae are accepted here. Phylogenetically the parent type was a stream-dwelling, trout-like fish. Of the four species of *Oncorhynchus* considered here, the coho is closest to the parent type while the pink represents an extreme in the opposite direction. Coho fry may move downstream in very large numbers after emerging from the gravel (Hoar, 1954) but they may also move upstream. In other words they wander about and are displaced by high water, becoming widely distributed in the river system from rather restricted spawning redds. They do not, however, usually leave the rivers during their first year although they may—like many of the trout—take up residence in lakes. Coho in fresh water are not strongly schooling fish. On the contrary, they show aggressive behaviour, selecting and defending territories and spacing themselves throughout the waters available to them. Important also is the fact that they are relatively inactive at night, settling at low light intensity rather than surfacing and becoming active.

Evolution of the sea-going behaviour in the salmonids and its progressive specialization to obligatory ocean dwelling types has involved three groups of changes: (a) smolt transformation, (b) increased nocturnal activity, and (c) schooling behaviour. These changes all occur to some extent in the present-day coho salmon just prior to downstream migration and are evident in many other anadromous salmonids.

The *smolt transformation* with its significant changes in cryptic coloration and the development of a resistance to sea water occurs in all North American genera and in many species of the Salmonidae. The biochemical and endocrinological changes have been described in some detail for Atlantic salmon (*Salmo salar*) and the literature reviewed in several places (Hoar, 1957; Pickford and Atz, 1957). Comparable physiological changes are indicated in the coho and sockeye. Behaviour changes in these species have already been summarized. In the genus *Oncorhynchus*, some species show a much abbreviated period of freshwater de-

pendence. Pinks and chums at one extreme are able to enter sea water as very young fry and are not known as mature freshwater populations. It is, in fact, extremely difficult to maintain these species in freshwater for more than two or three months after the normal time of migration. The assumption is that those biochemical differences which permit a freshwater salmonid to thrive in sea water are developed during the alevin or early fry stages of chum and pink salmon.

Nocturnal activity is characteristic of the behaviour of the downstream migrating salmon. This does not imply that all migration through lakes and rivers occurs during the night. It is a well known fact that mass movements of sockeye, for example, may be observed in some places during the day. The conditions responsible for such activity have not been described but, on the basis of the present study, it is suggested that the explanation will be found in conditions of temperature and the depth of the water. In many places—Port John, for example—migration is almost entirely nocturnal. A change in the diurnal rhythm of activity seems to be a part of the smolt transformation, at least in the case of the coho (Hoar, 1951, 1954).

In the course of specialization, nocturnal activity shows three features, (a) increased swimming at night, (b) surfacing at low light intensity and (c) a precise triggering of this behaviour with changing light intensity. These reach an extreme in the pink salmon fry. The precise triggering of activity with falling light intensity is well known to fisheries biologists, has been seen repeatedly in this work and is a behaviour with high survival value. When many small fish must face a fixed number of predators, the shorter and more precise the period of contact, the better will be their chances of survival. This sharp diurnal peak in time of downstream migration is particularly marked in the schooling species.

Schooling behaviour may have evolved as a by-product of this sharp "triggering" of the movements of masses of small fish. However, its presence in coho fry which have been displaced as a group in one way or another suggests that the reaction of staying close to other fish is strong in salmonids when they have no other reference points and will easily occur if these fish, displaced from the streams by high water, find themselves in lakes or estuaries. Its probable advantages in a pelagic life have been discussed (Keenleyside, 1955) and it would be expected to increase in intensity during the evolution of progressively more juvenile pelagic salmonids. As a significant mechanism in downstream migration, schooling is probably less important in fry than in smolts where a grouping reaction may be an important preliminary to the mass exodus from large areas of deep water.

Mechanics of Juvenile Salmon Migration

An attempt will be made in this section to describe the mechanism of migration in the four species as juveniles in freshwater. Many details have probably not yet been seen but what are considered to be the essential features, probably common to all species, were observed many times with groups of sockeye, chum or pink fry (but never coho fry) in the 360 cm. troughs.

As the light intensity falls in the late evening, fish (particularly sockeye) collect in the upstream area of the trough, emerging from among the stones and assembling there from other areas. The presence of a few actively swimming fish over the gravel at the inflow end of the trough appears to stimulate others to join them. Presently some members of the group drift downstream somewhat, losing position, whereupon others turn and swim with them (schooling reaction). The entire group then swims down the trough, actively oriented and travelling with the current. They are apparently stopped only by the end of the trough. Here they orient with the current and swim against it to the inflow end once more. After a moment they again lose position and the whole sequence is repeated. This activity may be watched until the light intensity is too low for observation. Journeys are orderly. In several tests chums were found to be travelling at the rate of 30 to 40 metres per hour while pinks travelled at 15 to 20 metres per hour. With reference to these rates of swimming it should be noted that under other conditions pinks may travel faster than chums (Hoar, 1958).

Activity such as this would result in some oriented downstream swimming. In nature the "end of the trough" is the ocean feeding grounds. In a river, however, conditions are far more complex and varied than in the troughs. Schools moving downstream probably orient and hold position for varying periods at points where flow conditions change radically or where different contours and depths of water alter the stimulus relationships. The mechanism of losing position and turning to swim with the moving group may be a basic feature. The amount of downstream swimming would also be expected to vary with the relative sensitivity of the eye and the characteristic responses of the different species to current. Downstream migration is usually nocturnal but it is probably a mistake to believe that visual stimuli are absent. The visual units of the salmon's eye respond to light of low intensity (Ali and Brett, MS.) and even during the night some visual orientation seems likely. The significant point is that reactions which orient fish both in the current and in their hiding places among stones during the day will be reduced at night—particularly when the fish rise toward the surface—and that fish losing direct contact with the bottom will swim or drift with the current.

The specific behaviour patterns and their steering components are related not only to migration but also to survival and success for varying periods in the rivers. The following seem to be the major contrasts with respect to the downstream migration and survival of the four species.

Coho fry. The downstream movement of coho fry is probably an "accidental" displacement of fish which settle somewhat but do not hide among the stones during the night. They display no increased activity at night but will be subject to some displacement, particularly in times of high water. They are maximally adapted for survival in shallow streams, displaying marked cryptic coloration, strong hiding reactions and a ready response to sudden changes in water current.

Pink fry. The pink salmon exemplifies the most extreme departure from

this stream dwelling type. It becomes intensely active at night, rising directly into the surface layer of the water. The response to current is relatively weak at all times. When pinks partially lose their visual contact with the river bottom they may swim rapidly with the current. Their exit from the river is prompt and their seaward migration seems to consist of a series of nocturnal leaps, rising at night and swimming vigorously, at least partly in an oriented downstream direction, and retreating from the light in the morning. This species is not adapted to feed and survive in shallow streams. Prior to schooling it may still hide among stones but thereafter its only protection is in the schooling flight reaction and a tendency to move to deeper waters in bright light. It lacks the camouflage of bottom dwelling fish.

Sockeye fry and underyearlings. The sockeye fry differs from the others in its small size and begins its life as an almost "planktonic" individual. It responds sharply and strongly to water currents when it can orient visually but, when it rises from the stones in the evening and becomes active, downstream movement is inevitable. Its migration may be entirely that of a displaced animal which wanders about in rapidly flowing water, or there may be a measure of active swimming with the current as in the case of the pink fry. What actually happens probably depends on the relative intensity of the orienting factors such as light, river bottom, and current. The recently emerged sockeye fry is well protected while in the streams, since it hides by day and is cryptically coloured besides.

Somewhat older sockeye fry show a change in reactions which seem to form the basis of an upstream migration. They hide less under stones (probably like coho and chum fry—only when startled), remain exposed at higher light intensities (Hoar *et al.*, 1957), and respond strongly to current even at higher temperatures (Keenleyside and Hoar, 1954). Larger fry will also be able to stem faster currents because of their size. Where visual orientation is possible and water currents not excessive these reactions would enable actively schooling fish to swim long distances upstream in shallow water. In deep waters the fish prefer intermediate depths during the day (Hoar, 1954) but still surface in the evening (Johnson, 1956).

Chum fry. The chum is the largest of the recently emerged fish and responds most strongly to current. It orients sharply to the current during the day and hides rapidly if disturbed. Its nocturnal migration may be less of a displacement than that of the recently emerged sockeye fry and less of an oriented downstream movement than that of the pink but this is speculation and, as with the other species, elements of displacement and active swimming probably combine in varying degrees depending on the relative strength of the various orienting factors such as current, temperature and visual reference points.

Smolts. The smolt transformation of the coho is associated with increased activity at all times, a greater tendency to school and a marked nocturnal activity. The latter evidently involves a change in photoresponses. A greater avoidance of bright light seems also to develop in sockeye at the time of the smolt transformation (Hoar, *et al.*, 1957, Table I). Both species preserve a strong hiding behaviour, retreating either to deep pools or among stones, when startled or

when the light intensity is high. These behaviour changes which have been catalogued at the time of smolt transformation are admittedly inadequate to account for the assembling of many small fish in a large lake or river and their precisely timed migration from it. The significance of the smolt transformation and the development of strong "internal motivation" is indicated but the details of physiology and related ethology remain to be studied. The actual mechanism of migration through a short river, such as Hooknose Creek, does not appear to differ greatly from that just described for the chum fry.

Speculation Concerning the Isolating Mechanisms

It is unlikely that one will ever be able to establish the phylogenetic sequence of behaviour associated with the seaward migration of *Oncorhynchus*. However, the present analysis suggests several probable steps and additional clues can be anticipated when the investigation is carried further and when other species of *Oncorhynchus* and other genera of salmon have been studied. For example, the Japanese masu (*O. masou*) represents a more trout-like form than the coho. Coloration and form of the fins (Kubo, 1953) strongly suggest a bottom dwelling fish. Landlocked stocks are well known and many of the males, even in areas with ready access to the sea, fail to migrate but mature successfully in fresh water (Anon., 1955). Again, some preliminary observations of the chinook salmon (*Oncorhynchus tshawytscha*) indicate that it may be an intermediate type between the coho and the chum since it seems to show less territorial activity than the coho fry and a positive response to sea water (K. Newman, unpublished) which is less intense than that of the chum.

Four steps are suggested in the separation of the species described here. A knowledge of the salinity relationships of the very young sockeye is basic to the postulated sequence. J. G. Hunter, of the Fisheries Research Board of Canada, in some unpublished experiments, found that sockeye fry could be readily adapted to sea water and, from its earliest stages, was much more resistant to salinity than the coho. Kathrine Newman, in the spring of 1956 and Dr. B. Baggerman in the spring of 1957, working at the University of British Columbia, found that both sockeye fry and sockeye smolts preferred hypertonic sea water to fresh water although the preference was more marked in the smolts. Further investigation is required but the indications are that the sockeye as a fry prefers sea water and is rather resistant to it.

The first step suggested is the separation of a type ancestral to the sockeye, pink and chum salmon but more like the sockeye than the other two. These species, because of their similarities in schooling behaviour, nocturnal activity, and early preference for sea water may have evolved from a common ancestral type. This ancestral type developed from trout-like salmonids of the present-day coho type but before the evolving genus *Oncorhynchus* had lost its ability to complete successfully its life cycle in fresh waters. At the present time, coho fry often move down rivers in the springtime by the thousands. At Port John they may be seen swimming to and fro in the tidal areas of the river mouth—sometimes in brackish water but not entering the sea at this stage. There are several

mechanisms (low water, high temperature) which might cause fish with such a behaviour to remain for progressively longer periods in brackish water and lead to the development of an early resistance to hypertonic solutions. The type ancestral to the schooling species of today may have lived for thousands of years in estuaries before they were able to live in hypertonic sea water during the fry stages. During this period they would be confined to brackish estuaries until the smolt transformation.

It is suggested that a second major step in evolution occurred before the smolt transformation was lost and perhaps before an obligatory marine life was necessary to the success of any species. It is assumed that at this stage some Pacific salmon had acquired the behaviour of migrating to the estuary as fry. Newly hatched Japanese *Plecoglossus* are carried into the estuaries as minute larvae by the rapidly flowing streams. When they have grown somewhat they migrate up the rivers and assume a bottom dwelling, territorial behaviour (Okada, 1955, pp. 56–57). The hypothetical salmon fry may have been carried into the estuaries in a similar manner and acquired a pelagic schooling behaviour which permitted survival and exploitation of the food resources of the estuary. In areas where lakes formed barriers or traps for these fry migrants, the sockeye habit would develop with a specialization in behaviour associated with the exodus from the lake in the smolt stage. Both the physiology of the smolt transformation and the specialized activity associated with the migration from lakes require much further study.

The third step visualized occurred in the estuary where the ancestral type with early fry migration acquired progressively earlier resistance to hypertonic sea water and an abbreviation of the pre-smolt period. Present-day pink and chum salmon lack the smolt transformation, are immediately able to enter sea water and do not—contrary to underyearling sockeye—lose their preference for sea water when retained in fresh water for several months after the fry migration (B. Baggerman, unpublished). An early loss of parr marks, the development of a silvery coloration and sea water resistance in the fry stage would favour successful exploitation and survival in the ocean.

The fourth step involves a split between the chum and the pink. This investigation indicates that the pink is the more specialized. Like the coho, the chum shows preference for certain localized areas, hides quickly when startled and retains some indication of the parr markings. The behaviour of the pink, as already described, results in a minimum of freshwater life. It is suggested that where the spawning areas of the rivers are short, shallow and rapid this line of specialization would be favoured. Survival would depend on the ability to enter seawater as fry and the behaviour associated with a prolonged survival in shallow rivers would be unnecessary.

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Heat Budget of the Water in the Vicinity of Triple Island, British Columbia[1]

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ABSTRACT

Meteorological and oceanographic data from 1947 to 1955 have been analysed and magnitudes of the terms of heat budget equation discussed. Both energy transfer and advective processes are important in the heat budget of water in northern British Columbia. Solar radiation has the largest annual amplitude, the minimum and maximum occurring in winter and summer respectively. Annual amplitude of evaporation is about one-half that of solar radiation, the maximum and minimum also occurring in winter and summer respectively. Heat loss by conduction of sensible heat from the sea is in phase with that by evaporation. Although heat loss by effective back radiation is large (100 g-cal./cm.^{2}/day) the annual amplitude is relatively small. The annual cycle of total heat transfer across the air–sea boundary is primarily governed by variation of solar radiation, evaporation, and conduction. It is quite marked, with maximum loss (approximately 350 g-cal./cm.^{2}/day) occurring during the short winter period (December, January) and maximum gain (approximately 200 g-cal./cm.^{2}/day) occurring during the long summer period (May to September). There was an apparent 25% loss of heat at the air–sea boundary during the period 1947 to 1954. Losses occurred every year except 1947. Appreciable year-to-year variations occurred in all components of the equation.

The total heat released to the atmosphere by condensation of water vapour is about fivefold that made available by conduction of sensible heat from the sea.

The large discrepancy in the rate of change of heat content of water with rate of heat exchange at the air–sea boundary is attributed to advection.

INTRODUCTION

During the past few years the coastal waters of British Columbia in Dixon Entrance, Hecate Strait, and Queen Charlotte Sound (Fig. 1) have been subjected to intensive oceanographic studies (Barber and Tabata, 1954). Series of quasi-synoptic surveys have been made at bi-monthly intervals throughout the year from May 1954 to June 1955. In addition, daily observations of surface sea temperature and salinity have been made at a number of locations in the region for more than 15 years (Hollister, 1952).

The study of the distribution of sea temperature in any locality is an important subject, whether it be in relation to the physical or the biological problems. Yet to present knowledge, there has been no examination of the various processes affecting sea temperature in this region. Such processes can conveniently be treated under the general heading of heat budget. Once the dominant factors affecting sea temperature are evaluated in the heat budget, it is possible to forecast, or at least recognize, some features of the distribution of temperature in these waters.

The sea temperature depends on energy exchange processes occurring at the air–sea boundary and advective processes occurring below sea surface. Solar

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radiation, effective back radiation, evaporation (and condensation), and conduction of sensible heat are included in the energy exchange processes. The advective processes are directly concerned with transport of water and are brought about by external forces such as winds, tides, and density differences of water masses. The water warms or cools depending on whether or not there is net transfer of heat into or out of the water in the area.

A general discussion of the heat budget of the sea is given in "The Oceans" (Sverdrup *et al.*, 1942). Since then, there have been numerous studies made by others (Jacobs, 1951; Anderson, 1952; Bretschneider, 1952; Schule, 1952; Jung, 1955; and Sparger, 1955). Of these, Anderson's work is notable in that observations were conducted with extensive instrumentation.

In this paper an attempt is made to examine the principal features of energy exchange at the air–sea boundary and of the heat budget of the water in the vicinity of Triple Island, and to discuss some of the consequences of the energy exchange and its relation to the seasonal variation of sea temperature in the region. The study forms a basis for the appreciation of the processes in the locality and a starting point for more detailed studies.

The present study is based mainly on data from Triple Island (54° 18′ N., 130° 53′ W., see Fig. 1) partly because they are most complete and partly because the region is centrally located and conclusions may be applicable to the general area of the surveys.

Data

The monthly means of dry- and wet-bulb temperature measurements, precipitation, clouds, and winds were determined from means of thrice-daily observations (1030, 1630 and 2230 P.S.T.—Time Zone U), except those from observations during 1947 and 1948 which were made only twice daily (1030 and 1630 P.S.T.). Cloud amounts and wind speeds were estimated. These data were extracted from Canada Department of Transport records (Meteorological Division, 1947–1955).

The monthly mean sea temperatures were determined from daily observations of temperature at a depth of 3 feet at the time of the daylight high tide. Each day's observation is about 45 min. later than the previous one. The time of observation progresses through the day from about 0700 to 1900 hours in about two weeks. The monthly values were obtained from reports on observations of sea water temperature and salinity on the Pacific Coast of Canada (Pacific Oceanographic Group, 1947–1955).

Bathythermographic data of the region were based on six surveys (in May, July, August, 1954; February, April, June, 1955) made during the Hecate Project (Pacific Oceanographic Group, 1955a). Unpublished data from Lightship *Swiftsure* and Weather Station "P" (Pacific Oceanographic Group, 1955b) have also been referred to.

Heat Budget of the Sea

The heat budget of a column of water in the sea depends principally on Q_o, short-wave radiation of the sun and sky, both direct and diffuse,

Q_r, its reflected radiation from the sea,
Q_b, effective back radiation (long-wave radiation from sea surface minus that from the atmosphere),
Q_e, evaporation (and condensation),
Q_h, conduction of sensible heat between the atmosphere and sea,
Q_v, net amount of heat brought in or out by transport of water (advection),
Q_θ, the amount of heat used locally for changing the temperature of sea water (heat storage).

Sverdrup *et al.* (1942) expressed the heat budget in any time interval (Δt) as

$$Q_o - Q_r - Q_b - Q_e - Q_h + Q_v - Q_\theta = 0.$$

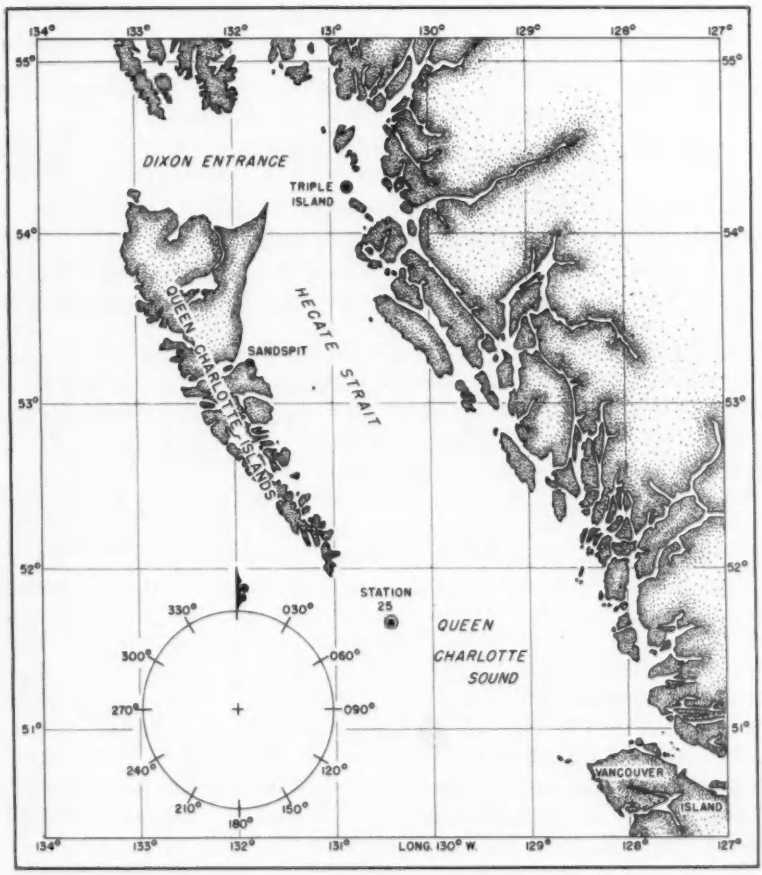

FIG. 1. Chart showing location of Triple Island, B.C., Oceanographic Station 25 and general oceanographic regions of Dixon Entrance, Hecate Strait, and Queen Charlotte Sound.

The units can be conveniently chosen as gram-calories per square centimetre per day (g-cal./cm.²/day).

This equation assumes that transformation of kinetic energy to heat, heating due to radioactivity, chemical and biological activity, and transfer of heat through the sea floor, may be neglected.

Radiation from the Sun and Sky Absorbed by the Sea (Q_s)

The ultimate source of energy for atmospheric processes and their accompanying processes in the sea is the sun. The radiation that impinges on the earth's surface is mostly short-wave and reaches the surface partly as direct radiation from the sun and also as reflected or scattered radiation from clouds and atmospheric particles. Kimball (1928) has evaluated the total amount of radiation received on the sea surface under cloudless skies at different localities. In this study the values for solar radiation were obtained by linear interpolation from his tables. Angstrom's formula,

$$Q_t = Q_o\,(1-0.071C) \text{ in g-cal./cm.}^2\text{/day},$$

where Q_t is the solar radiation reaching the sea surface after clouds have been taken into consideration,

Q_o is the total incoming radiation per day under clear sky, and

C is the amount of clouds in scale 0 to 10,

is used to correct for cloud cover. Sverdrup *et al.* (1942) consider this formula satisfactory for computation of monthly or annual mean values, but not for shorter intervals.

The amount of radiation which is reflected from the sea surface depends primarily on the sun's altitude and on atmospheric turbidity. It also depends to some extent on the roughness of the sea surface but this phenomenon is not well understood (Anderson, 1952). Anderson's reflectivity values are used because they are considered to be most reliable.

After reflectivity has been taken into account, the absorbed portion of solar radiation (Q_s) is left, and it is this energy that warms the sea.

Table I shows the data and the calculated values of incident and absorbed solar radiation at Triple Island. The computed values are also illustrated in Fig. 2(a). Although the incident energy, which has a minimum of 105 g-cal./cm.²/day in December and a maximum of 825 g-cal./cm.²/day in June (Fig. 2(a)(i)) is potentially available under cloudless skies, cloud conditions in this locality are such that only one-half of this energy reaches the sea surface (Fig. 2(a)(ii)) and is subsequently absorbed into the sea (Fig. 2(a)(iii)). It is evident that cloud cover is a major influence in the process of solar radiation reaching the sea. The annual cycle of the absorbed energy is in phase with that of the total incident solar energy under cloudless skies, reaching a minimum (35 g-cal./cm.²/day) in December and a maximum (350 g-cal./cm.²/day) in June.

The monthly mean values of absorbed solar radiation follow the general cyclic trend of the grand monthly means but there are appreciable year-to-year fluctuations. These fluctuations can conveniently be illustrated by using the

TABLE I. Calculated mid-monthly values of absorbed solar radiation at Triple Island, B.C., (54°N. 131°W.) and the contributing factors.

	Jan.	Feb.	Mar.	Apr.	May	June	Jul	Aug.	Sep.	Oct.	Nov.	Dec.
Q_o	132	242	420	612	762	825	770	645	482	295	160	105
C	7.20	7.55	7.15	6.95	7.55	7.65	7.60	6.95	6.95	7.95	7.95	8.10
Q_i	65	112	207	310	354	377	353	327	244	128	70	45
$\bar{h}$	9.5	14.5	24.0	27.5	31.5	32.5	31.0	29.0	24.0	18.0	11.5	8.5
r	0.17	0.13	0.09	0.08	0.07	0.07	0.07	0.08	0.09	0.11	0.16	0.19
Q_s	54	97	188	285	329	350	328	300	222	114	59	36

Q_o = Total solar radiation (g-cal./cm.²/day) incident on sea surface in absence of clouds (interpolated from Kimball's (1928) table).

C = Clouds in tenth of sky covered—monthly averages from Meteorological Records between 1947 and 1954.

Q_i = Incident solar radiation according to Angstrom's formula (g-cal./cm.²/day).

$\bar{h}$ = Mean mid-monthly sun's altitude (degrees).

r = Proportion of solar radiation reflected from sea surface under above ($\bar{h}$, C) conditions. (From Anderson's (1952) chart).

Q_s = Absorbed solar radiation (g-cal./cm.²/day).

standard deviations of the monthly means as shown in Fig. 2 (a)(iii). Although the percentage variations of monthly means are not too different it is evident that magnitudes of the fluctuations are largest in summer and smallest in winter These year-to-year fluctuations of the monthly means are no doubt due to the variations in cloud cover.

EFFECTIVE BACK RADIATION (Q_b)

The sea surface is to some degree a black body and therefore emits long-wave radiation in proportion to the fourth power of the absolute temperature. Most of this is absorbed by the atmosphere which in turn re-radiates long-wave radiation back to the sea; but part of this is reflected back to the atmosphere. The net transfer of these energies is called effective back radiation and is a function of sea and air temperatures, vapour content of the air, and cloud amount and height.

The radiation from the sea surface is expressed by

$$Q_c = \epsilon_w \sigma \theta_s^4,$$

where Q_c = long-wave radiation from the sea surface in g.cal./cm.²/day,

ϵ_w = emissivity factor for water = 0.970 and is independent of water temperature and dissolved solids (Anderson, 1952),

σ = Boltzmann constant = 1.175×10^{-7} g-cal./cm.²/day/degree⁴, and

θ_s = absolute temperature of the surface sea water.

Probably the most complete study to date on atmospheric radiation (Q_a) is that by Anderson (1952) who related the ratio of this to black body radiation at temperature θ_a as a function of cloud height and amount, and vapour pressure. His empirical formula is

$$\frac{Q_a}{\sigma \theta_a^4} = a + be_a$$

where θ_a = absolute temperature of the air above the sea surface, and
e_a = vapour pressure (mb.) of the atmosphere where the air temperature is measured.

The constants a and b are related to cloud height (high, middle, low) and amount (scattered—1/10 to 5/10; broken—6/10 to 9/10; overcast—10/10). Anderson has prepared several charts relating

$$\frac{Q_a}{\sigma\theta_a^4}$$

linearly to e_a for these nine cases. These are based on Lake Hefner studies, and may be different at other localities. However, lacking better information, it is assumed that the relations are applicable to the data observed at Triple Island, at least to the first order of approximation.

Combining these, the effective back radiation may be written

$$Q_b = Q_c - (1 - K)\, Q_a$$

where K is the proportion of atmospheric radiation reflected from the sea surface and is equal to

$$1 - \epsilon_w = 0.030.$$

Therefore the final expression for this radiation (Q_b) becomes

$$Q_b = 1.141[\theta_s^4 - \theta_a^4\,(a + be_a)]\ 10^{-7}\ \text{g-cal./cm.}^2\text{/day.}$$

Figure 2(b) shows the grand monthly means computed from this formula. The annual amplitude of this radiation is small compared to that of solar radiation and the extremes seldom vary more than 25% of the annual mean. The heat loss from sea surface by this process varies from a maximum of 130 g-cal./cm.^{2}/day in winter, more than twice the magnitude of the absorbed solar energy, to a minimum of 85 g-cal./cm.^{2}/day in summer, when it is less than one-third of the absorbed solar energy.

The year-to-year fluctuations of the monthly means are small (Fig. 2(b)) in most cases, except in January when it is twice that of other months. This is due to the tremendous heat loss in January 1950, when the sky was relatively clear and the air temperature was low.

Evaporation (Q_e)

It may be shown that evaporation from the sea is dependent on the vertical gradient of vapour pressure and eddy conductivity above the sea surface. However, the difficulty of observing these terms makes this approach impractical, at least with present-day instrumentation. Consequently, most of the computations of evaporation are based on mass transfer theory. Anderson (1952) compared computations by theoretical methods of Sverdrup (1937) and Sutton (1949) with his observations and showed that they agreed well.

Using measurements made at 20 m. height above the mean sea surface at Triple Island, Sverdrup's evaporation formula becomes

$$Q_e = 4.70(e_s - e_a)\, u_a \quad \text{g-cal./cm.}^2\text{/day}$$

where e_s = vapour pressure (mb.) of saturated air at sea surface,
e_a = observed vapour pressure (mb.) of air at height a cm. above the sea surface, and
u_a = wind speed (m./sec.) at height a cm. above the sea surface.

The data resulting from this formula are shown in Fig. 2(c). There is a marked annual cycle in the heat loss associated with evaporation, the maximum (175 g-cal./cm.²/day) occurring during winter and the minimum (25 g-cal./

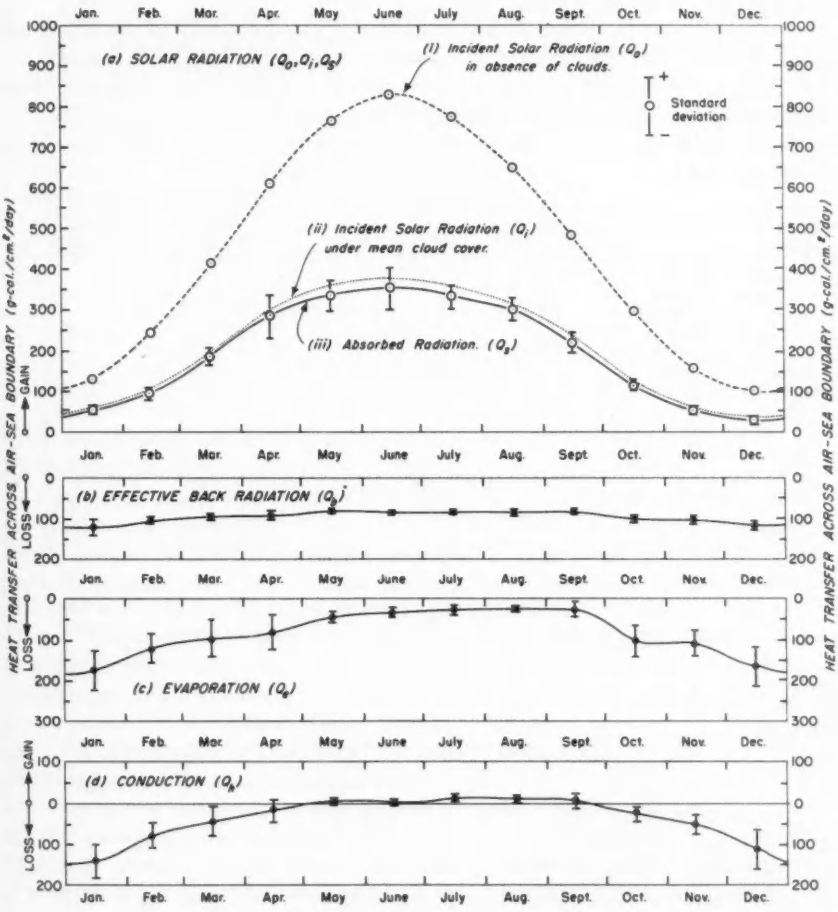
Jan. Feb. Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec.
(a) SOLAR RADIATION (Q_o, Q_i, Q_s)
(i) Incident Solar Radiation (Q_o) in absence of clouds.
Standard deviation
(ii) Incident Solar Radiation (Q_i) under mean cloud cover.
(iii) Absorbed Radiation. (Q_s)
HEAT TRANSFER ACROSS AIR-SEA BOUNDARY (g-cal./cm.²/day)
GAIN
LOSS
(b) EFFECTIVE BACK RADIATION (Q_b)
(c) EVAPORATION (Q_e)
(d) CONDUCTION (Q_h)

FIG. 2. Grand monthly means (1947–1954) with standard deviations of
(a) Solar radiation (Q_o, Q_i, Q_s),
(b) Effective back radiation (Q_b),
(c) Evaporation (Q_e), and
(d) Conduction of sensible heat (Q_h) at Triple Island.

cm.²/day in summer. Its annual amplitude is approximately one-half of that of absorbed solar radiation.

The year-to-year fluctuations of the monthly mean values of evaporation are appreciably large, particularly in the period October to April as shown in Fig. 2(a). Very large deviations occurred in some months as in March 1951 and April 1954, when the values were comparable to the maxima observed in January of these years. Examination of meteorological data revealed that the former was due to the presence of a cold air mass over the area and the latter was associated with strong winds.

Jacobs (1951) has made an over-all assessment of evaporation over the whole north Pacific, and for seasonal evaporation in the northeast Pacific (54° N., 140° W.) has obtained the values shown in Table II (a). Comparison of these values with those from Triple Island (Table II (b)) indicates that the values resulting from the present study are on the average 20% larger than those found by Jacobs.

TABLE II. Seasonal evaporation, northeast Pacific Ocean and Triple Island, B.C.

	Dec. Jan. Feb.	Mar. Apr. May	Jun. Jul. Aug.	Sep. Oct. Nov.
(a) Northeast Pacific Ocean (54°N., 140° W.) (Jacobs, 1951) (g-cal./cm.²/day)	120	60	30	90
(b) Triple Island (1947–1954) (54°N., 131°W.) (g-cal./cm.²/day)	155	75	40	85

It may be pointed out that when the sea surface is warmer than the air above it, the air is warmed and becomes unstable. This gives rise to convection currents which facilitates evaporation. This will be the case in winter. Oceanographic processes also aid evaporation during colder months by setting up a convection current below the sea surface. This is accomplished by surface cooling which results in descent of surface water and upward transfer of warmer water from underneath. In summer the sea is colder than the air above it, and the air becomes stable. Under such conditions evaporation is retarded. Furthermore, in coastal waters the stability of water is increased by surface warming and by dilution of surface water by addition of fresh water from river runoff. During summer months the efficiency of evaporation is therefore decreased.

Condensation occurring at the sea surface would transport heat into the sea. For this process to occur, the air immediately above the sea surface must be sufficiently moist and also warmer than sea surface. In such cases the stability of the air is increased and turbulence reduced. This would hinder such a process and it is doubtful if condensation has any major significance in transporting heat to the sea. The present data did not show any evidence of condensation immediately above the sea surface.

CONDUCTION OF SENSIBLE HEAT (Q_h)

The transfer of sensible heat between the sea and atmosphere is dependent mainly on the vertical temperature gradient and eddy conductivity above the

sea surface. As in the case of evaporation, eddy terms are difficult to measure, so conduction is usually computed by means of the Bowen Ratio (R) (Bowen, 1926). This term is the ratio of the heat transferred by conduction to that transferred by evaporation. Thus, knowing evaporation, sensible heat transfer may be computed.

The Bowen Ratio is

$$\frac{Q_h}{Q_e} = \frac{0.61\ (T_s - T_a)}{(e_s - e_a)}$$

where T_s = sea temperature (°C.) and
T_a = air temperature (°C.).

At present there is some controversy over the validity of this ratio (Montgomery, 1940; Sverdrup, 1943), due to the neglect of radiative diffusivity (Brunt, 1944), turbulence, and effect of spray upon evaporation; but no critical information is available.

The grand monthly means of the Bowen Ratios computed from this formula are shown in Fig. 3. The annual cycle is apparent, having a maximum (+ 0.8)

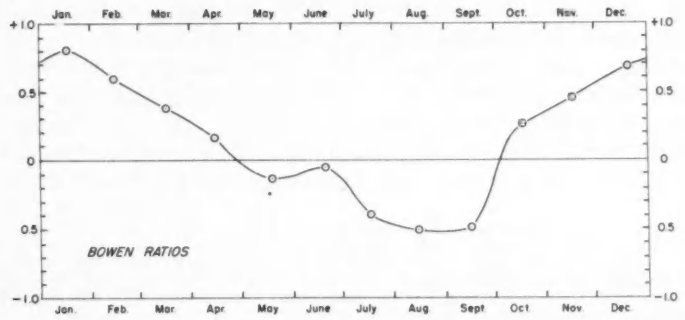

FIG. 3. Grand monthly means (1947–1954) of Bowen Ratios at Triple Island.

in winter and a minimum (− 0.5) in summer. The constant ratios assumed by early investigators (Mosby, 1936; McEwen, 1938) because of lack of suitable data, are no longer considered valid as pointed out by Jacobs (1951). The present results substantiate his conclusions.

The values of evaporation, Q_e (Fig. 2(c)) were multiplied by these ratios (Fig. 3) to determine the monthly transfer of sensible heat, and are shown in Fig. 2(d). The energy given off from sea to atmosphere as sensible heat is large in winter and reaches its maximum (145 g-cal./cm.^{2}/day) in January. It is relatively small during warmer months and is directed into the sea during late summer at a rate of less than 15 g-cal./cm.^{2}/day.

During the period November to March, conduction from sea to atmosphere is relatively large but during the remaining months it is negligible compared to contributions of heat transfer from other processes.

The annual cycle of conduction is similar to that of evaporation though smaller in amplitude. The combined influence of evaporation and conduction is much larger than that of the solar radiation during the winter, therefore during the cold winter months these cooling processes have a dominant role in changing sea temperature.

The same argument applies in conduction as in evaporation that heat transfer by conduction is more efficient in winter when the air is colder than the sea.

The year-to-year fluctuations of the monthly mean values of conduction are almost as large as those of evaporation; in fact, the magnitudes of deviations are larger than grand monthly values of warmer months.

Total Heat Released to Atmosphere by Condensation of Water Vapour and by Conduction of Sensible Heat from the Sea

When water vapour in the atmosphere condenses as precipitation or to form clouds, latent heat is made available as sensible heat to warm the atmosphere. But the heat released in forming the clouds can be neglected because the same amount is required when clouds dissipate by evaporation. Thus the order of magnitude of the net transfer of heat by condensation to the atmosphere in the general area can be estimated from precipitation records.

The heat transferred to the atmosphere was computed as the precipitation multiplied by the latent heat of vaporization, 585 g-cal./gram (since the amount of snowfall is small, the heat of fusion is neglected). These values, the sensible heat conducted from the sea, and the heat derived from evaporation, are shown in Table III. There is an annual cycle in the heat of precipitation from a minimum

Table III. 1947–1954 data at Triple Island, B.C.

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
(a) Mean monthly precipitation and consequent heat released to the atmosphere												
Precipitation (cm./day)	0.38	0.42	0.31	0.30	0.21	0.20	0.20	0.24	0.32	0.56	0.52	0.62
Heat (g-cal./cm.²/day)	222	246	181	176	123	117	117	140	187	328	304	362
(b) Sensible heat conducted from the sea to the atmosphere												
(g-cal./cm.²/day)	144	77	43	20	−4	−3	−12	−9	−3	27	51	116
(c) Heat derived from the sea by evaporation												
(g-cal./cm.²/day)	174	122	94	88	45	60	31	26	32	109	110	166

of 115 g-cal./cm.²/day in June and July to a maximum of 360 in December. The Table shows that energy released by condensation greatly exceeds (5 times) that from conduction and is greater than the heat derived from the sea by evaporation. Comparison of Tables III (a) and I reveals that in the winter months the heat made available by precipitation is even greater than that from solar radiation. This indicates that the precipitation may be a significant factor in moderating the winter climate in this region.

Total Heat Transfer across the Air–Sea Boundary

The total transfer of heat across the air–sea boundary is evaluated in Fig. 4 as the arithmetic sum of the values of terms illustrated in Fig. 2. The principal feature of the annual cycle is that the greatest loss, of the order of 350 g-cal./cm.^{2}/day, occurs in the winter period of December and January, and the greatest gain, more than 200 g-cal./cm.^{2}/day, occurs in the longer summer periods from

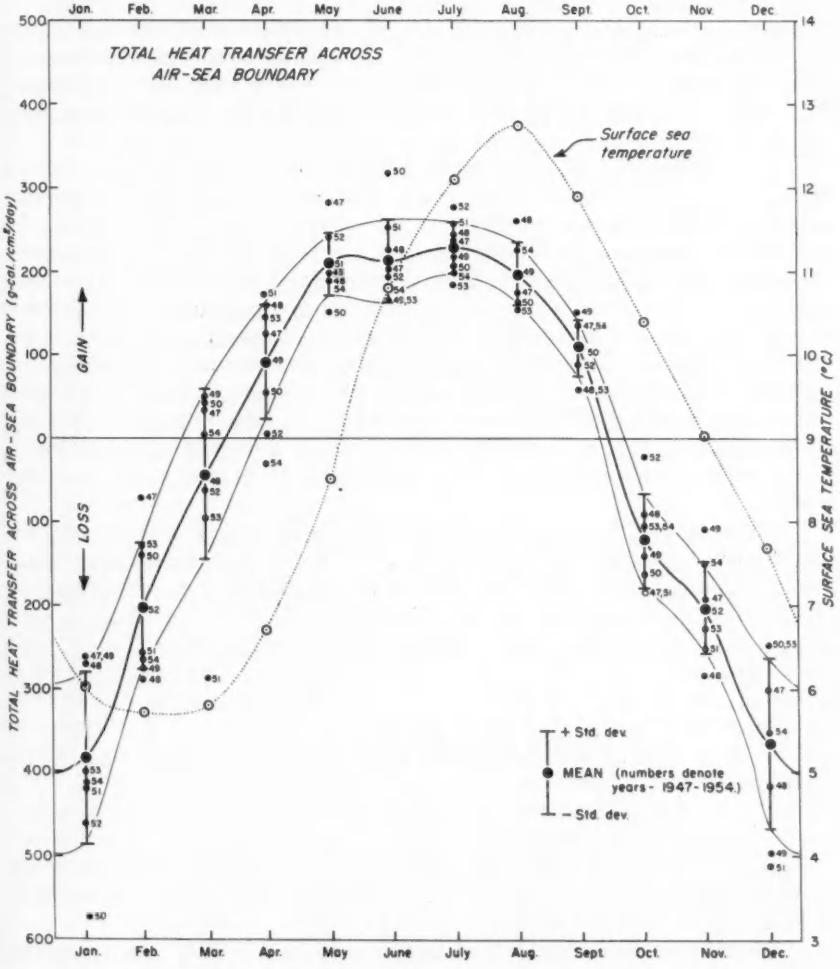
TOTAL HEAT TRANSFER ACROSS AIR-SEA BOUNDARY
Surface sea temperature
GAIN
LOSS
TOTAL HEAT TRANSFER ACROSS AIR-SEA BOUNDARY (g-cal./cm.²/day)
SURFACE SEA TEMPERATURE (°C)
+ Std. dev.
MEAN (numbers denote years - 1947-1954.)
- Std. dev.
Jan. Feb. Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec.

Fig. 4. Grand monthly means (1947–1954) with standard deviations of total heat transfer across air–sea boundary at Triple Island. Grand monthly means of surface sea temperature at Triple Island during same period are also shown.

May to September. The periods of no net transfer occur during the latter part of March and September.

The monthly means of the total heat transfer of the individual years follow the general cyclic trend of grand monthly means. However, there are appreciable differences in the year-to-year deviation of monthly means as shown in Fig. 4. It will be seen that deviations during the half-year period between October and March inclusive are, on the average, twice ($\pm$ 80 g-cal./cm.^{2}/day) those during the remaining half-year ($\pm$ 40 g-cal./cm.^{2}/day). Variations of more than 200 g-cal./cm.^{2}/day as in January 1950 and March 1951 are exceptionally large. Because of the year-to-year fluctuations, the periods of no net transfer vary. In spring it may occur during the five weeks between early March and early April but in autumn it occurs in the shorter period from late September to early October.

All components of the total heat transfer across the air–sea boundary exhibit annual cyclic characteristics. The largest component is solar radiation (Q_s) which is always positive (heat enters the sea). The second is due to evaporation (Q_e) of which the amplitude is about half as large and is always negative (heat leaves the sea). Conduction (Q_h) is in phase with evaporation but has a slightly smaller amplitude. It is positive in summer and negative in winter and the net heat loss through the year is about half of the loss due to evaporation. The sum of the amplitudes of these two components is comparable and the annual cycle is opposite in phase to that of solar radiation. Effective back radiation (Q_b) is always negative but its amplitude is only about one-tenth that of solar radiation. Thus the seasonal variation of total heat transfer is primarily governed by annual cycles of the input of solar radiation and the output of heat by evaporation and conduction.

In general the efferent energy components, that is, evaporation, conduction, and effective back radiation, are greatest in winter when the afferent component, insolation, is at a minimum. These conditions are extreme from mid-November to mid-January. At this time the heat loss due to effective back radiation alone (Fig. 2 (b)) is greater than solar radiation under cloudless skies (Fig. 2(a)(i)). Hence there is no possibility of the water being warmed from energy exchange at the air–sea boundary. In presence of cloud cover, insolation is reduced (Fig. 2(a)(iii)) so that heat loss occurs during the four months from mid-October to mid-February. During the first and last month of this period warming of water from energy exchange processes is possible but improbable.

The occurrence of cloudless skies is rare during winter, but when it occurs, it is usually associated with the presence of a cold polar air mass with low moisture content and strong northerly winds. This condition is ideal for heat loss by all three efferent components. The large heat loss in January 1950 is an example of this.

The standard deviations of these components (Fig. 2) show that during the period October to March, the year-to-year deviations in the total heat transfer are due mainly to variations of evaporation and conduction, and during the period May to July to modification of solar radiation by cloud cover.

The periods of no net transfer of heat occur in spring and autumn when efferent and afferent components are equal in magnitude. During these periods solar radiation, evaporation, and conduction have similar deviations. Since cloud cover accounts for the large variation of solar radiation, and winds and differences of vapour pressures and temperatures above the sea surface mainly affect evaporation and conduction, these factors determine the time of occurrence of these periods.

During the warmer months from April to September, solar radiation takes the leading role in the total heat transfer across the sea surface. Evaporation becomes secondary and conduction becomes of minor concern. During this period, cloud cover is the most restrictive influence. For example, in June the heat input under cloudless skies is about 700 g-cal./cm.^{2}/day and under, say 8/10 cloud cover, it is about 300 g-cal./cm.^{2}/day. The large range in the variation in June (Fig. 2(a)(iii) and 4) further illustrates this point.

The mean yearly gain of heat across the air–sea boundary during the period 1947–1954 was 30,600 g-cal./cm.^{2} and the mean loss 39,300 g-cal./cm.^{2}, resulting in a net loss of 25%. Losses occured in most years except in 1947 when there was a gain of 20% (Table IV). The greatest loss of 20,900 g-cal./cm.^{2} (50%) occurred in 1951.

By using values of standard deviations, it is possible to draw extreme cases. If all the positive fluctuations are considered, the gain is 1½ times the loss and if all the negative fluctuations are considered the loss is more than twice the gain. It is unlikely that such extremes occur often but these values suggest that there can be very large variations in the heat gain and loss in this locality.

Limitations

The accuracy required for these conclusions depends on the purposes for which they are to be used, and to the range of fluctuations within each month. The accuracy obtainable from the computations depends on accuracy of theories, the reliability of data, and the magnitude of random and systematic errors. Lacking direct measurements, the evaluation of such errors is difficult and only some of these can be estimated.

Table IV. Total annual transfer of heat energy at air–sea boundary at Triple Island, B.C., (1947–1954). (Units in g-cal./cm.^{2}.)

Year	Gain	Loss	Difference	% Gain or loss
1947	35,600	29,200	+ 6,400	+20
1948	35,000	42,200	− 7,200	−19
1949	30,200	37,500	− 7,300	−22
1950	30,800	39,800	− 9,000	−25
1951	31,500	52,400	−20,900	−50
1952	26,900	39,200	−12,300	−37
1953	27,200	35,600	− 8,400	−27
1954	27,400	38,200	−10,800	−33
Mean	30,600	39,300	− 8,700	−25

The values of cloud cover (tenths) used in computation of insolation, and wind speeds (miles per hour) used in the computation of evaporation, were estimated. An error of one-tenth in the estimate of cloud cover will give rise to an error of 15% in the values of insolation. Errors of 15% are possible in the estimate of winds; consequently, the evaporation values may be in error by 15%. These errors are for individual observations; however, by taking monthly averages the random errors have been reduced to a minimum. There still remain the systematic errors but these are not well known.

The computation of heat transfer due to evaporation, conduction, and effective back radiation all depend on the difference of air and sea temperatures. Both air and sea temperatures were observed in daytime, the two being taken in a different manner. Both of these temperatures are representations of daytime values and are not true means. But since differences are used, the errors are assumed to be small.

In the computation of effective back radiation the assumption was made that Anderson's formula for atmospheric radiation based on Lake Hefner data was applicable to data from Triple Island. This implies that the composition (water vapour, carbon dioxide, ozone content) of the atmosphere in the two localities is similar. Although errors may be introduced from such an assumption, they are considered to be small since large differences in composition from place to place are unlikely.

Anderson (1952) has concluded that even when all the terms of the heat budget equation are measured with the best of present day accuracy, the maximum accuracy obtainable from the energy budget equation is $\pm 5\%$. It may be concluded that there is a possibility of the error as large as 20%. This figure is of the same order as the apparent heat loss from the air–sea boundary through the eight years (1947–1954).

As shown in Table IV there seems to be a consistent loss of heat during these years. Thus it is likely that there was a net loss of heat (heat storage Q_s becomes negative) from the sea surface during these years, but the absolute magnitudes of these are open to question.

Relation between Total Heat Transfer across the Air–Sea Boundary and Annual Cycle of Surface Sea Temperature

A comparison of the annual cycle of the total heat transfer across the air–sea boundary with the annual cycle of surface sea temperature indicates that the rise and fall of temperature occur about one month before the time inferred from heat transfer (Fig. 4). If the heat transfer is considered to occur only at the sea surface, and if the surface sea temperature can be assumed to be indicative of total heat content in a column of water affected by this heat transfer, then the minimum and maximum temperatures should occur at periods when there is no net heat transfer; that is, during the latter part of March and September respectively. The reason for this is that the rate of change of heat content of the water column is a function of the integral of the total heat transfer.

Neither the minimum nor the maximum surface sea temperature occurs at these periods; instead, the temperature begins to rise in late winter when the

sea is actually losing heat to the atmosphere at a rate of about 100 g-cal./cm.^{2}/day and begins to fall in late summer when the sea is gaining heat at a mean rate of about 150 g-cal./cm.^{2}/day. In the former the heat loss is sufficient to cool a column of water 50 m. deep by about 0.6 degree Centigrade per month, while in the latter the gain is enough to warm it by 0.8 degree per month. It is probable that this discrepancy is due to the contribution of heat transfer due to advective and eddy processes. There are two likely possibilities; one is vertical transfer of heat from deeper water, and the other is lateral transport of water. In winter, it is probably due to transfer of warmer water from the greater depths to the surface, or transport of warmer water into the region, or a combination of both. In summer, it is attributed to the exchange of heat with colder water in the greater depths, or intrusion of cold water into the region, or a combination of both.

This leads to the consideration of advection.

Heat Transfer by Advection (Q_s)

There is no reason to believe that the spring and autumn periods mentioned in the preceding section are the only times at which advections are important; in fact, it may be more influential at other periods. However, its influences are probably more easily recognized during these two periods.

Regularly taken bathythermographic data are available from the vicinity of Triple Island for the period May 1954 to June 1955 and the advective terms will be discussed on the basis of the heat budget during this period. The monthly means of total heat transfer at the air–sea boundary at Triple Island and composite sea temperatures from Stations 54, 55, 56, and 57 (Fig. 6) are shown in Fig. 5(a) and 5(b). It is apparent that there are two main thermal structures during the year, the stratified layers occurring during the summer from May to September, and a well-mixed layer that appears to increase in depth progressively from about 50 m. in October to about 150 m. in April. There are no temperature data during the winter between September and January. Therefore the isotherms are interpreted from those of southern Hecate Strait (Station 25—see Fig. 1) and although the regions are separated by about 100 miles it is assumed that the temperatures are approximately representative of winter thermal structure. The stratified layers occurred during the period when there was a net gain of heat at the sea surface, while the mixed layers occurred during the period when the sea was losing heat to the atmosphere.

Figure 5(b) also suggests that the heat content of the water column in August was less than in July. There was also some indication of a relatively large amount of heat in the water during the late autumn and winter when the sea was losing heat to the atmosphere.

Now, the rate of change of heat content (storage) of a column of water of unit cross-sectional area and z cm. deep may be calculated as

$$Q_s = \frac{\partial}{\partial t}\int_0^z \rho\, c_p\, \partial T\, \partial z \simeq \frac{\overline{\rho c_p}\int_0^z \partial T\, \partial z}{\partial t}$$

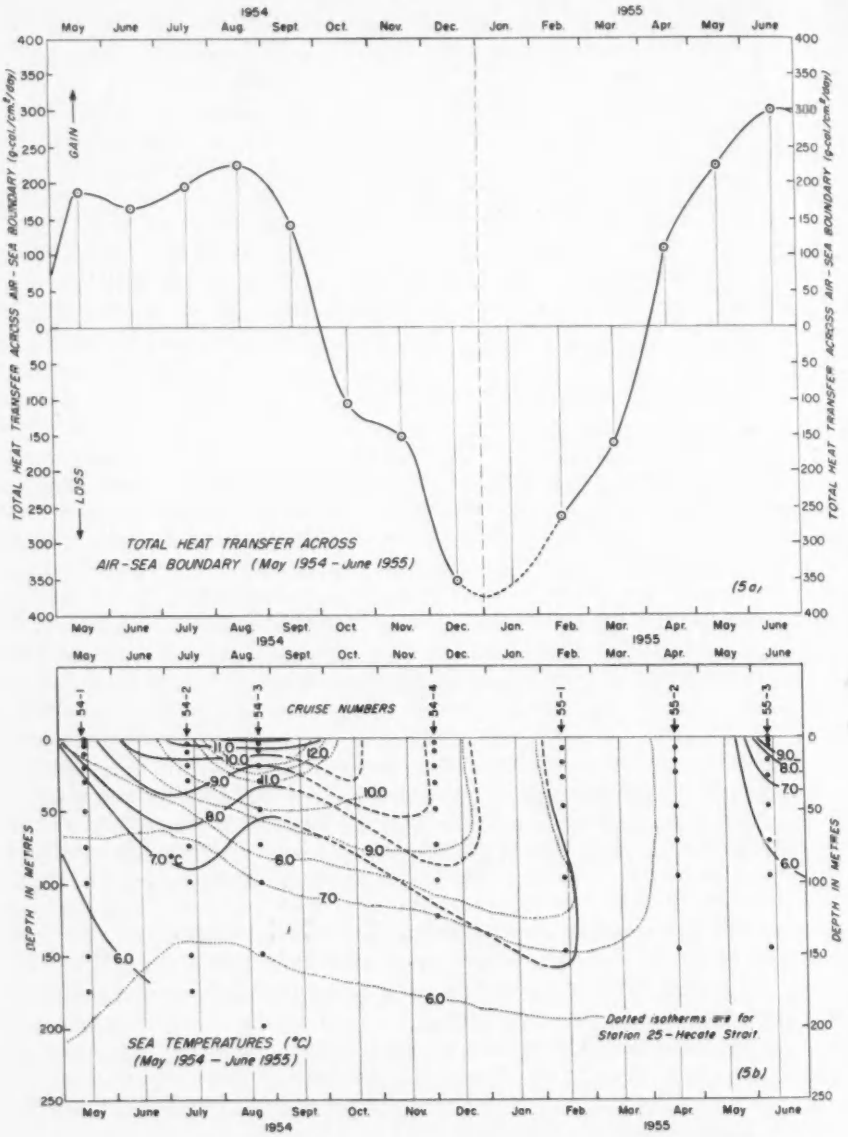

FIG. 5. (a) Monthly means of total heat transfer across air–sea boundary at Triple Island during the period May 1954 to June 1955.

(b) Sea temperatures in the water adjacent to Triple Island during the same period. (Temperatures observed on the same day at Stations 54, 55, 56 and 57 (see Fig. 6) are averaged and are indicated in the figure under cruise numbers.) No observations were made here during Cruise 54-4. Interpolated values from Station 25 (see Fig. 1) are used.

where Q_θ = change of heat content (g-cal./cm.^{2}/day),
ρ = density of sea water (g./cm.^{3}),
c_p = specific heat of sea water (cal./g.),
T = temperature of sea water (°C.),
z = depth of column of sea water above which major change of heat content occurs (cm.).
$\bar{\rho}$ = mean density of sea water (g./cm.^{3}),
$\bar{c_p}$ = mean specific heat of sea water (cal./g.),
∂t = time interval in days, and
$\partial T \partial z$ = area bounded by the two temperature–depth curves.

The mean density of sea water in the water column in this locality is about 1.025 g./cm.^{3} and its specific heat 0.938 cal./g. Thus the equation becomes

$$Q_\theta = \frac{0.962 \int_0^z \partial T \partial z}{\partial t}$$

During the period from May to July, 1954, the heat content in the whole Dixon Entrance–Chatham Sound region increased by about 370 g-cal./cm.^{2}/day (Table V(a); see Fig. 6 for station positions). But during the same time interval the sea received heat through the surface at a mean rate of 180 g-cal./cm.^{2}/day. This was only half as much as the actual increase of heat content. This suggests that warm water intruded the region. This may have come from the south through Hecate Strait, from the ocean by way of Dixon Entrance, or from both.

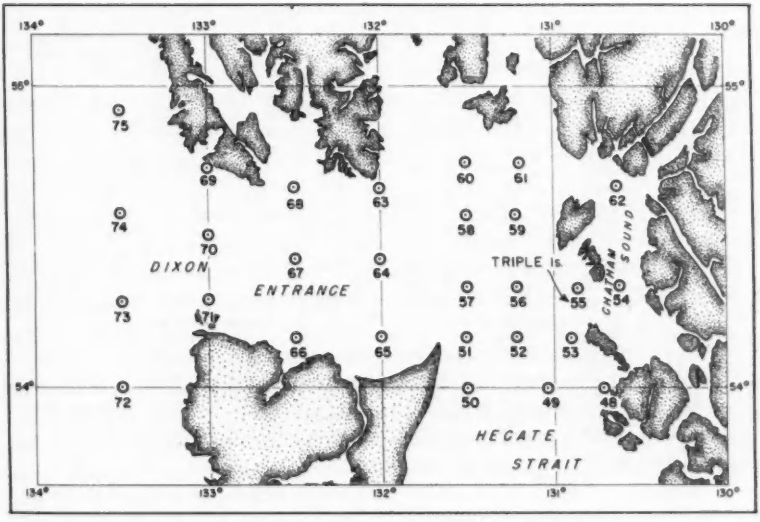

FIG. 6. Chart showing station positions in Dixon Entrance and Northern Hecate Strait.

TABLE V. Loss or gain of heat in Dixon Entrance. (Units in g-cal./cm.²/day.)

Station (see Fig. 6 for position)	Depth (*m.*)	Depth interval (*m.*)	Loss(−) or Gain(+)	Depth interval (*m.*)	Loss(−) or Gain(+)
(a) Period between 12 May–14 July, 1954					
51	20				
52	20				
53	110	0–80	+380	...	...
54	170	0–150	+390	...	...
55	230	0–200	+700	...	...
56	80	0–50	+190	...	...
57	160	0–100	+260	...	...
58	130	0–120	+340	120–130	− 10
59	120	0–100	+510	...	...
60	120	0–100	+340	...	...
61	270	0–230	+520	230–250	0
62	260	0–150	+240	150–250	> − 10
63	180	0–160	+580	...	...
64	310	0–90	+220	90–280	− 70
65	80	0–50	+290	...	...
66	70	0–70	+190	...	...
67	370	0–90	+ 90	90–300	− 40
68	180	0–150	+370	...	...
69	200	0–170	+420	...	...
70	370	0–150	+180	150–360	− 20
71	460	0–230	+410	230–460	− 10
72	170	0–140	+620	140–165	− 20
73	350	0–140	+490	140–300	−100
74	370	0–190	+420	190–320	0
75	170	0–130	+300	130–165	0
Mean gain (mostly in upper 160 m.)			+370		
Mean loss			−10		
Net gain			+360		

Depth interval (*m.*)	Loss(−) or Gain(+)	Depth interval (*m.*)	Loss(−) or Gain(+)
(b) Period between 14 July–23 Aug., 1954			
0–10	+ 10	10–80	−260
0–200	−280	...	...
0–100	−500	100–230	−100
0–10	+ 20	10–50	− 60
0–20	+ 70	20–100	− 60
0–30	+ 10	30–50	− 20
0–100	−410	...	...
0–15	+ 20	15–100	−220
0–110	−550	100–250	> − 10
0–20	+ 20	20–250	−190
0–15	+ 50	15–165	−260
0–150	+210	150–280	0
0–20	+ 30	20–80	− 40
0–55	+140	55–70	− 10
0–290	+280	...	...
0–20	+ 70	20–75	−110
0–15	+ 30	15–170	−250
0–60	+100	60–150	+ 10
0–110	−180	110–460	+ 90
Mean gain			+ 60
Mean loss			−180
Net loss			−120

Station (see Fig. 6 for position)	Depth (*m.*)	Depth interval (*m.*)	Loss(−) or Gain(+)	Depth interval (*m.*)	Loss(−) or Gain(+)
(c) Period between 23 Aug. 1954–13 Feb., 1955					
51	20				
52	20				
53	110	0–80	− 60	...	...
54	170	0–50	− 50	50–175	+ 80
55	230	0–60	− 50	60–200	+ 20
56	80	0–50	− 50	...	...
57	160	0–80	− 80	80–100	+ 10
58	130	0–80	− 80	...	...
59	120	0–60	− 60	60–100	+ 10
60	120	0–70	− 50	70–100	+ 10
61	270	0–40	− 40	40–250	+ 80
62	260	0–30	− 40	30–250	+130
63	180	0–80	−100	80–150	+ 20
64	310	0–60	− 90	60–280	+ 80
65	80	0–80	− 90	...	...
66	70	0–70	− 80	...	...
67	370	0–60	− 60	60–250	+ 50
68	180	0–80	−180	80–180	+ 40
69	200	0–80	− 90	80–200	+ 60
70	370	0–60	− 70	60–150	+ 20
71	460	0–60	− 40	60–250	+ 60
72	170				
73	350				
74	370				
75	170				
Mean loss (mostly in upper 60 m.)			− 70		
Mean gain			+ 40		
Net loss			− 30		

Depth interval (*m.*)	Loss(−) or Gain(+)	Depth interval (*m.*)	Loss(−) or Gain(+)
(d) Period between 13 Feb.–14 Apr., 1955			
0–100	−110		
0–150	−360		
0–200	−350		
0–80	− 10		
0–150	−130		
0–300	−290		
0–80	−110		
0–70	−110		
0–350	−390		
0–180	−290		
0–200	−260		
0–370	−350		
0–460	−380		
0–300	−490		
0–310	−380		
Net loss	−270		

TABLE V (cont'd)

Station (see Fig. 6 for position)	Depth (*m.*)	Depth interval (*m.*)	Loss(−) or Gain(+)	Depth interval (*m.*)	Loss(−) or Gain(+)
(e) Period between 14 Apr.–17 June, 1955					
51	20				
52	20				
53	110	0–110	+110		
54	170	0–160	+170		
55	230	0–200	+140		
56	80	0–80	+160		
57	160	0–150	+180		
58	130	...	...		
59	120	...	...		
60	120	...	...		
61	270	...	...		
62	260	...	...		
63	180	...	...		
64	310	0–90	+180	90–280	−40
65	80	0–80	+190		
66	70	0–70	+180		
67	370	0–120	+200	120–200	−10
68	180	0–115	+240	115–180	−30
69	200	0–110	+230	110–200	−20
70	370	0–130	+270	130–200	−10
71	460	0–100	+180	100–460	−80
Mean gain (mostly in upper 100 m.)			+190		
Mean loss			− 20		
Net gain			+170		

During the period between July and August the situations were in contrast. This time there was a general decrease (Table V(b)) in the heat content in the region of 120 g-cal./cm.²/day while the heat received at the surface was 230 g-cal./cm.²/day (Fig. 6(b)), the decrease generally occurring in the layer between 20 and 150 m. This cooling is attributed mainly to transport of cold water into the region. This could be cold, upwelled oceanic water from the vicinity of Dixon Entrance.

Between August 1954 and February 1955 the decrease in heat content (Table V(c)) at depths generally above 60 m. in the Dixon Entrance–Chatham Sound region is about 70 g-cal./cm.²/day while in the whole column (to depths as great as 280 m.) the decrease is of the order of 30 g-cal./cm.²/day (Table V(c)). Since the mean rate of loss of heat at the sea surface was about 150 g-cal./cm.²/day, then during this interval there must be a transport of warm water into the region in order to satisfy the discrepancy of 80 g-cal./cm.²/day. An examination of the winds at Triple Island (Fig. 7(d–k)) during this period showed that during September to February southeast winds were most frequent. It seems reasonably certain that the region was supplied with warm water from the south through Hecate Strait and from offshore.

During February and April, 1955, the decrease of the heat content (Table V(d)) was more than twice as much (270 g-cal./cm.²/day) as that lost from the sea surface (110 g-cal./cm.²/day). Probably this was due to some transport of cold water to the region from the north or northwest, since the oceanic waters

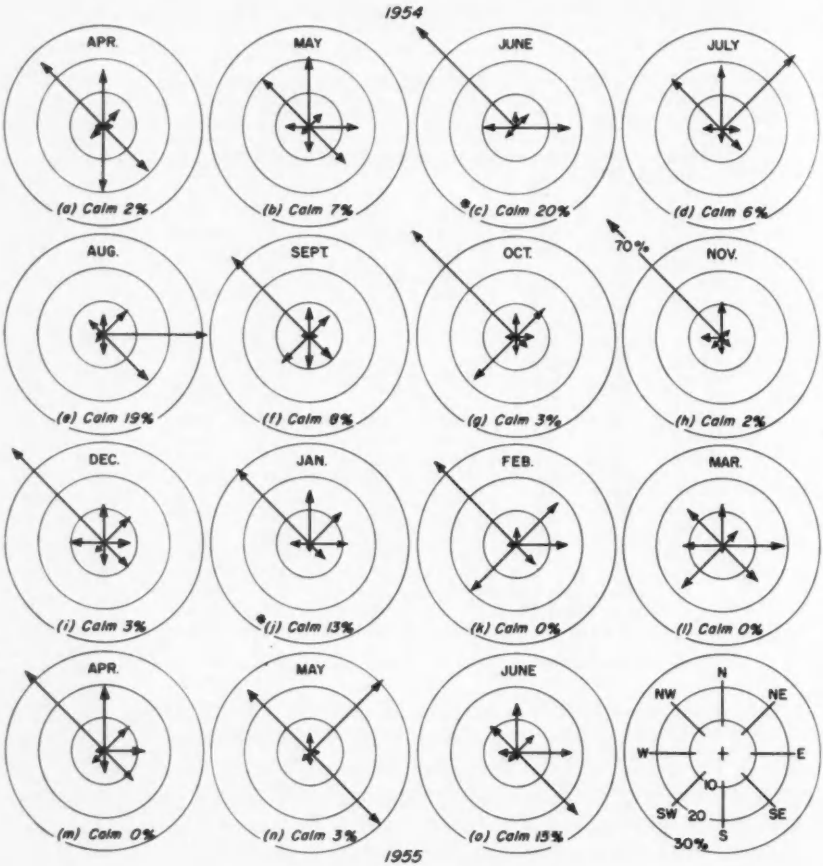

FIG. 7. Wind roses in percentage of frequencies at Triple Island during the period April 1954 to June 1955. Arrows indicate direction to which wind is blowing. (*In roses (*c*) and (*j*) data from Sandspit (Fig. 1) are shown, owing to lack of Triple Island records for June 1954 and January 1955.)

south and southwest of Dixon Entrance were warmer. In the period April to June, 1955, the increase in heat content (Table V(e)) at a depth generally above 100 m. was of the order of 190 g-cal./cm.^{2}/day and about 170 g-cal./cm.^{2}/day through the whole column (Table V(e)). This amount is slightly less than what can be accounted for by heat transfer (220 g-cal./cm.^{2}/day) at the sea surface. The difference appears to be due to intrusion of cold oceanic water in the greater depths.

A comparison of the changes of heat content of the waters in Dixon Entrance, Swiftsure at the entrance of Juan de Fuca Strait (48°30′ N., 125° 00′ W.), and Ocean Weather Station "P" (50° N., 145° W.) reveals some interesting features (Table VI). The magnitudes of the rate of heat transfer at the sea surface at

Triple Island appear to be more comparable to the rate of increase and decrease of heat content at Ocean Station "P" than to those of nearer coastal regions. This suggests that the advective terms are more important to the heat budget of the local waters than in the open ocean at Station "P".

TABLE VI. Comparison of total heat transfer across air–sea boundary at Triple Island, B.C., and loss or gain of heat from the waters of Dixon Entrance, Swiftsure, and Ocean Station "P." (Units in g-cal./cm.²/day.)

	1954		Aug. 1954 to Feb. 1955	1955	
	May–June	July–Aug.		Feb.–Apr.	Apr.–June
Total heat transfer across air–sea boundary at Triple Is.	+180	+230	−150	−110	+220
Heat loss (−) or gain (+)					
(a) Dixon Entrance	+370	−120	− 30	−270	+190
(b) Swiftsure	No data	−100	− 30	− 30	+ 70
(c) Station "P"	+220 (+280 in upper 60 m.)	+320 (+240 in upper 30 m.)	−140 (−180 in upper 60 m. +40 between 60 to 150 m.)	−170 (upper 150 m.)	+190 (upper 150 m.)

SUMMARY

Only some one-half of the solar energy reaches the sea because of persistent cloudy skies in the Triple Island region. The annual cycle of solar radiation is quite marked, the maximum input (350 g-cal./cm.²/day) occurring in summer and the minimum (35 g-cal./cm.²/day) in winter. The annual cycle of heat loss from the sea to the atmosphere by effective back radiation is relatively small and varies from the maximum (130 g-cal./cm.²/day) in winter to the minimum (85 g-cal./cm.²/day) in summer. The annual cycle of heat loss by evaporation is marked, with the maximum (170 g-cal./cm.²/day) occurring in winter and the minimum (25 g-cal./cm.²/day) in summer. Seasonal values of evaporation are about 20% larger than those evaluated by Jacobs for the northeast Pacific Ocean. The annual cycle of conduction of sensible heat from the sea to the atmosphere is in phase with that of evaporation. The maximum loss (145 g-cal./cm.²/day) occurs in winter and the maximum gain, though of much smaller magnitude (10 g-cal./cm.²/day), occurs in summer. Bowen Ratios have been used to compute conduction of sensible heat from the sea to the atmosphere. They were found to vary from +0.8 in winter to −0.5 in summer. Errors involved in the computations are unknown but they may be as large as 20%.

The annual cycle of total heat transfer across the air–sea boundary is quite marked with the maximum loss (about 350 g-cal./cm.²/day) occurring in a short period (December and January) in winter and the maximum gain (about 200 g-cal./cm.²/day) occurring in the longer period (May to September) in summer. The periods of no net transfer occur in the latter part of March and September. Since largest amplitudes of the annual cycle of the components of heat transfer are due to solar radiation and the combination of evaporation and conduction,

which are opposite in phase, these terms primarily govern the seasonal variation of heat transfer across the air–sea boundary.

There was an apparent heat loss of about 25% from the sea surface during the period 1947–1954. Losses occurred every year except in 1947 when there was a gain of about 20%.

The total heat energy released to the atmosphere by condensation of water vapour is about fivefold that made available by conduction of sensible heat from the sea to the atmosphere. In winter this is greater than the heat derived from solar radiation.

Comparison of the total heat transfer at the air–sea boundary at Triple Island and rate of change of heat content of the water in the vicinity during May 1954 and June 1955 was made. The excess increase in the heat content between May and July, 1954, is probably due to inshore transport of warmer water from the south. The decrease in the heat content during July and August, 1954, is attributed to inshore transport of cold oceanic water. Between August 1954 and February 1955 the decrease in the heat content was much smaller than would be expected from the loss occurring at the sea surface. This is believed to be due to warmer oceanic water entering the region through Hecate Strait and Dixon Entrance. During February to April, 1955, intrusion of cold water from the north is suspected. The influence of advection on the heat budget of the water was small during April to June, 1955.

Besides energy transfer processes, advective processes also play an important role in affecting coastal sea temperatures.

ACKNOWLEDGMENTS

The author wishes to express his acknowledgments to the lightkeepers of Triple Island, without whose conscientious efforts in first observing the data the study would not have been possible; to Mrs. M. A. Smith for carrying out the tedious calculations; to Mr. L. M. McKenzie for drawing the illustrations, and to the other members of the Pacific Oceanographic Group for general assistance. He is indebted to Mr. W. H. Mackie of the Canada Department of Transport for making available the unpublished meteorological data and finally to Dr. J. P. Tully for his helpful criticisms.

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Solar Radiation Penetrating the Ocean. A Review of Requirements, Data and Methods of Measurement, with Particular Reference to Photosynthetic Productivity[1]

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INTRODUCTION

This review is intended to be introductory rather than comprehensive. Only those aspects of submarine and surface illumination which have a direct bearing on photosynthetic productivity in the sea are discussed in detail and most of the references are European and American in origin. No attempt has been made to include many papers that contribute little other than purely local data as such papers are of limited interest and would unduly lengthen the article.

The opportunity is taken to discuss, briefly, some of the measurements made by physiologists interested in the visual stimuli of zooplankton and fish.

Throughout, illumination will be expressed in the energy–time unit: langlies/minute. No one unit is ideal but such a multiplicity of units occurs in the literature that comparison of data becomes very tedious. The more commonly encountered units are defined and a list of conversion factors is given to assist the reader, but in all cases data from the literature have been converted into langlies/minute

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using the best practical estimate of conversion factors. The results, in some instances, may not be highly precise but are sufficiently so for the purpose of illustration.

Section I: Definitions and Conversion Factors

DEFINITIONS

1. Total Intensity of a Source ($M.L.^2T^{-3}$)

This is the total energy emitted in unit time from a source of radiant energy. The units commonly used are *watts, joules per second* or *gram-calories per minute.* For luminous intensity the unit is the *standard candle* which, unlike the energy units, implies a definite spectral distribution of the radiant energy. Intensity can also be expressed as the *number of radiation quanta of energy of specified wavelength emitted per second.* In photochemical work it is sometimes expressed as the *number of einsteins per minute*, the einstein unit being the radiant energy of specified wavelength absorbed at unit quantum efficiency by one gram-molecule of matter.

2. Energy per Area ($M.T.^{-2}$)

This is the total radiant energy falling on unit area. The concept is not used in photometry but is useful when considering energy balances or the total possible amount of photosynthesis.

The unit most commonly employed is the langley (see Aldrich *et al.*, 1947), abbreviated to ly.:

one langley = one 15° gram-calorie of energy/$cm.^2$

The energy per area can also be expressed by the number of radiation quanta of energy of specified wavelength entering a unit area or the number of einsteins of specified wavelength entering a unit area.

3. Energy Flux of a Source ($M.L.^2T^{-3}$)

This is the energy emitted from a source into unit solid angle in unit time. The energy units are the same as given in paragraph 1 above.

For luminous flux the source is the standard candle and the flux is called the lumen, ideally:

$$\frac{1 \text{ candle}}{4\pi}$$

4. The Illumination from a Source ($M.T.^{-3}$)

The term illumination is best applied only to light from a standard candle or a source of closely related spectral distribution (see p. 456). Illumination is flux per unit area and is commonly expressed in energy terms as *watts per square centimetre* or *langlies per minute* (ly./min. = gram-cal./$cm.^2$/min.). The number of quanta per minute per square centimetre, etc., can be used if the wavelength is specified. When the standard candle is the source:

1 phot = lumen/$cm.^2$
1 lux = lumen/$m.^2$
1 foot-candle = lumen/sq. ft.

The use of the term "lux" is recommended for illumination, and "langlies per minute" for radiation in general.

5. Brightness of a Source ($M.T^{-3}$)

This is the intensity of a source per unit area of source.

6. Absorption Coefficient (L^{-1}): k° or k

If λ is the wavelength of a monochromatic source, I_0 the initial illumination (or energy per unit time and area), I the attenuated illumination after the radiation has passed through a length dl of attenuating medium,

$$dI_\lambda = I_\lambda \times k^\circ \times dl$$

and if the absorption coefficient, k°, is unaltered through a distance l, the Lambert Law states that:

$$\ln I_{0\lambda} - \ln I_\lambda = k^\circ \times l.$$

l is generally expressed in metres for oceanographic measurements.

The Lambert Law is not valid when a multichromatic source of diffuse light is used. Atkins and Poole (1933) have defined a term "*vertical* absorption coefficient" for submarine measurement which will be represented here by k. This constant is used in an expression of the same form as the Lambert Law to characterize the removal of radiation with vertical depth, irrespective of the angle of incidence of the radiation I_0 and despite the fact that light will generally be attenuated by a process of scattering as well as true absorption. k values thus measured will tend to be larger near the sea surface than at greater depths and the variation of k down through homogeneous water will depend on the water mass concerned and the spectral range of the light. In practice, if measurement is restricted to light of waveband width less than 1000–500 Å, fairly constant k values can be obtained provided that the value of l is not too great.

An approximate conversion of the "vertical absorption coefficient" to the correct Lambert constant, or vice versa, may be attempted if the "mean path length" of light through the sea is known. This is the mean value of the path lengths that a light quanta must travel to descend one metre vertically. Whitney (1938a) has computed mean path lengths of solar radiation in pure water for any combination of sun angle and percentage of diffuse sky light. The mean path lengths vary with the wavelength of light. Unfortunately there are rarely sufficient data recorded in the literature to enable one to convert vertical absorption coefficients to the Lambert coefficients, although this would be desirable if the properties of various water masses were to be compared with precision. The additional complication of increased mean path lengths due to scattering within the water itself has been discussed by Whitney (1941) and an equation has been derived. As yet insufficient data are available for general application of this equation.

7. Extinction Coefficient (L^{-1}): κ° or κ

This coefficient is the constant used in the Lambert Law in paragraph 6 above but when base 10 logarithms are used:

$$\log I_{0\lambda} - \log I_\lambda = \kappa_\lambda{}^\circ \times l$$

l is again generally expressed in metres. There is a corresponding vertical extinction coefficient, analogous to the vertical absorption coefficient.

Use of these constants is to be encouraged as it makes for easier arithmetic. The nomenclature of these Lambert coefficients is still far from standard. In this review the vertical extinction coefficient will be written κ, and the true extinction coefficient κ°.

8. TRANSMITTANCE

If T_λ is the percentage of the incident illumination that passes one metre of uniformly attenuating media:

$$\kappa = \log\left(\frac{100}{T_\lambda}\right) ; \text{or } \kappa^\circ = \frac{1}{l}\log\left(\frac{100}{T_\lambda}\right)$$

If the medium remains uniform to a depth of l metres:

$$\text{percentage transmission} = 100 \times \left(\frac{T_\lambda}{100}\right)^l \text{ at a depth of } l \text{ metres.}$$

This expression is useful for some calculations.

NOTE ON ILLUMINATION UNITS

The use of units based on the standard candle is to be discouraged now that instruments for measuring radiant energy are easily available. Unambiguous information can be given by stating "illumination" in terms of ly./min., watts/cm.^{2}, quanta/cm.^{2}/sec., etc. *together with* a statement of the wavelength of the radiation used or the band width and band "centre of gravity" of a multichromatic light source if this is employed.

The standard candle unit is mainly useful for visual comparisons of illuminations having the same spectral characteristics as the standard candle. The illumination efficiency of a given energy rating is widely different with various light sources. The term "lux", etc. should, strictly, not be used unless one is describing light which has the same spectral characteristics as a standard candle. In practice, the terms lux or foot-candle are used for daylight, yellow or greenish lights and lamps, etc., where the peak intensity is in the neighbourhood of the wavelength of maximum visual response. For "coloured" light these terms are practically meaningless. The term "illumination unit" should then be used in place of candle. This unit would be defined as the intensity of light of the wavelengths in question emitted from a standard candle. However, a statement of energy intensity and spectral composition serves the same purpose and is more fundamental.

CONVERSION FACTORS

1. GENERAL

1 watt	= 1 joule/sec.
1 watt/cm.^{2}	= 1 joule/sec./cm.^{2}
1 watt	= 14.3 cal./min.
1 watt/cm.^{2}	= 14.3 ly./min.
1 ly./min.	= 0.0698 watt/cm.^{2}

1 ft-cdl.	= 10.76 lux
1 lux	= 0.0929 ft-cdl.
$\kappa°$	= 0.434 $k°$
$k°$	= 2.30 $\kappa°$

Near the sea surface:

$$\kappa° = \kappa \times \frac{100}{x}$$

where x is the mean path length in centimetres.

$$1 \text{ ly.} = 2.11 \times 10^{15} \times \text{Å quanta/cm.}^2$$

where Å is the wavelength of the quanta in Ångstrom units.

$$1 \text{ ly./min.} = 2.11 \times 10^{15} \times \text{Å quanta/cm.}^2\text{/min.}$$

$$1 \text{ ly.} = 3.50 \times 10^{-9} \times \text{Å einsteins/cm.}^2$$

$$1 \text{ ly./min.} = 3.50 \times 10^{-9} \times \text{Å einsteins/cm.}^2\text{/min.}$$

$$1 \text{ einstein/cm.}^2\text{/min.} = \frac{2.86 \times 10^8}{\text{Å}} \text{ ly./min.}$$

2. Langleys per minute, of Various Wavebands, as a Fraction of the Total Solar Radiation

The following gives approximate factors for multiplying the noon solar radiation energy between wavelengths 3000 and 50,000 Å, as measured by an Eppley Pyrheliometer (ly./min.$_T$), to give the langleys per minute in the wavebands shown. This assumes a clear sky and an unobscured sun, with the sky light contributing about one-third of the total radiation.

Waveband	Factor
3800–7200 Å	ly./min. = 0.5 ly./min.$_T$
3800–4900 Å	ly./min. = 0.17 ly./min.$_T$
4900–5600 Å	ly./min. = 0.12 ly./min.$_T$
5600–6200 Å	ly./min. = 0.085 ly./min.$_T$
6200–7200 Å	ly./min. = 0.12 ly./min.$_T$

The range 3800–7200 Å is slightly in excess of total visible radiation, and embraces the wavelengths of photo-synthetic activity. For more exact values compute from data of List (1951) or Rabinowitch (1951).

3. Candle Units of Illumination to Energy Units

The amount of radiant energy in one candle unit of illumination will depend on the spectral characteristics of the source. The following equations give the relationship when the standard candle is the light source and when daylight is the source.

(a) Relation when the light source has the standard luminosity curve.

1 lumen	$= 1.5 \times 10^{-3}$ watt.	1 watt	= 665 lumens
1 lux	$= 1.5 \times 10^{-7}$ watt/cm.^{2}		$= 2.15 \times 10^{-6}$ ly./min.
1 ft-cdl.	$= 1.6 \times 10^{-6}$ watt/cm.^{2}		$= 2.3 \times 10^{-5}$ ly./min.
1 watt/cm.^{2}	$= 6.6(5) \times 10^6$ lux		$= 6.2 \times 10^5$ ft-cdl.
1 ly./min.	$= 4.6(5) \times 10^5$ lux		$= 4.3 \times 10^4$ ft-cdl.

(b) RELATION FOR THE VISIBLE (AND PHOTOSYNTHETIC) RANGE OF NOON SUN PLUS SKY LIGHT (λ = 3800–7200Å)

1 lumen	$= 4.1(5) \times 10^{-3}$ watt.	1 watt = 240 lumens
1 lux	$= 4.1(5) \times 10^{-7}$ watt/cm.^{2}	$= 6.0 \times 10^{-6}$ ly./min.
1 ft-cdl.	$= 4.6 \times 10^{-6}$ watt/cm.^{2}	$= 6.5 \times 10^{-5}$ ly./min.
1 watt/cm.^{2}	$= 2.4 \times 10^{6}$ lux	$= 2.2(5) \times 10^{5}$ ft-cdl.
1 ly./min.	$= 1.6(75) \times 10^{5}$ lux	$= 1.5(5) \times 10^{4}$ ft-cdl.

NOTE. The energy units in 3(b) above should be doubled if the illumination relationship is required in terms of the total radiant energy between 3000 and 50,000 Å, as measured by an unfiltered pyrheliometer.

Data in 3(b) can be computed more exactly for various meteorological conditions and narrower wavebands from the Smithsonian Tables (see, for example, Table I). Data for other spectral distributions, such as that for the light at depth

TABLE I. Radiant energy in various wavebands as a percentage of the total energy between 3,500 and 7,500 Å. Surface perpendicular to sun's rays. Air mass=2. (Calculated from data in Smithsonian Tables, 9th Ed., 1954.) For the percentage of the total energy as measured by a pyrheliometer multiply these figures by 0.53, the approximate fraction of the energy between 3000 and 22,000 Å that lies in the range 3,500 to 7,500 Å.

Waveband (Ångstroms)	Energy	Waveband (Ångstroms)	Energy
	%		%
3500–3600	0.524	5500–5600	3.010
3600–3700	0.653	5600–5700	2.998
3700–3800	0.775	5700–5800	2.985
3800–3900	0.946	5800–5900	2.954
3900–4000	1.095	5900–6000	2.957
4000–4100	1.469	6000–6100	2.967
4100–4200	1.798	6100–6200	2.957
4200–4300	1.925	6200–6300	2.972
4300–4400	2.142	6300–6400	2.993
4400–4500	2.449	6400–6500	2.983
4500–4600	2.651	6500–6600	2.970
4600–4700	2.818	6600–6700	2.952
4700–4800	2.955	6700–6800	2.934
4800–4900	3.046	6800–6900	2.663
4900–5000	3.088	6900–7000	2.650
5000–5100	3.080	7000–7100	2.800
5100–5200	3.054	7100–7200	2.330
5200–5300	3.028	7200–7300	2.230
5300–5400	3.028	7300–7400	2.583
5400–5500	3.034	7400–7500	2.551

in the ocean, must be computed by direct measurement with a light source of known lumen value and spectral composition. *Very approximate* values for light at depth in the ocean can be obtained by using the data in 3(a) above.

Section II: Requirements

PHOTOSYNTHESIS

The literature on photosynthetic requirements is extensive and only some of the more important work having a direct bearing on marine production will be discussed in this Section.

1. Wavelength Requirements

The wavelength limits of photosynthetically active radiation are discussed fully by Rabinowitch (1951). There is little evidence for utilization below a wavelength of about 3700 Å. Radiation of a wavelength less than 3000 Å is highly injurious, although Gerloff *et al.* (1950) showed that blue-green algae could be exposed to ultraviolet radiation of 2750 Å for a sufficient time to kill all bacteria and still leave most of the algae viable. Little if any solar radiation of wavelength less than 3000 Å will penetrate to the ocean surface. The long-wave radiation limit is given by Emerson and Lewis (1943) as 7300 Å for *Chlorella*, although the exact limit is in some doubt and longer wavelengths may still have some effect (Rabinowitch, 1951). However, little error can be incurred if we assume that only light between the wavelengths of 3800 and 7200 Å (a slightly broader range than the visible) is effective for the photosynthetic production of plant substances in the ocean.

The relative efficiency of utilization of light of various wavelengths has been the subject of numerous investigations. No extensive generalization is possible as the behaviour of plants depends upon their pigment contents, but it appears that all the visible radiation can be used and it generally is used. The total amount of radiant energy is, however, more important than its wavelength (Stanbury, 1931; Jenkins, 1937; etc.).

The reason for this is explained by the many studies made on "action spectra" (Emerson and Lewis, 1942; Haxo and Blinks, 1946 and 1950; Levring, 1947; Tanada, 1951; Yocum and Blinks, 1954; Blinks, 1955). When the curve showing relative amount of photosynthesis for a constant number of quanta plotted against wavelength is compared with the *in vivo* light absorption curve of a plant a remarkable similarity is found. Chlorophyll is present in all marine plants and *must be present for photosynthesis to occur*. In green algae, chlorophyll is the predominant pigment and the relative photo-synthetic efficiency closely follows the chlorophyll absorption curve, having maxima at 4350 and 6750 Å and a marked minimum at 5500 Å. An appreciable fraction of submarine light energy is therefore wasted by these plants. Most marine phytoplankton, however, are like the brown algae and contain, in addition to carotene and chlorophyll, fucoxanthin and similar pigments which extend absorption and photosynthetic activity up to 5600 Å and enable a much more efficient utilization of white light. It follows that light energy must be transferred from the carotenoid pigments, where it is absorbed, to chlorophyll, where it is used for photosynthesis (Emerson and Lewis, 1942; Dutton, Manning and Duggar, 1943). This "transfer" of energy has been the subject of much investigation and may be of the order of 70% effective (cf. Rabinowitch, 1956). All workers find a slight decrease in photosynthetic efficiency around 4800–4900 Å which may be due to ineffective absorption or to a photo-oxidative effect of the carotinoids offsetting photosynthesis.

The red and blue-green algae contain pigments such as phycoerythrin phycocyanin, the chromoprotein phycobilins, which, together with the carotenoids present, absorb and cause a uniformly high photosynthetic efficiency

throughout almost the entire visible spectrum. With these algae, however, the action spectra show a sudden decrease at wavelengths greater than about 6500 Å, corresponding to the long-wave chlorophyll absorption peak. In these remarkable plants the chlorophyll, although essential, has lost its ability to bring about synthesis from the light that is absorbed by it directly. Energy transfers for this type of algae have been treated theoretically by Arnold and Oppenheimer (1950) and it has been shown that nearly all the quanta absorbed by the red pigments can be transferred to the chlorophyll. The inactivation of chlorophyll to the light absorbed directly occurs only in white light and if red light alone is used the plants can adapt and eventually make use of it (Yocum, quoted by Blinks, 1955).

A considerable amount of chromatic adaptation is possible in phytoplankton (cf. Stanbury, 1931, for *Nitzchia*) but there is no significant change in the pigment composition of lake plankton with depth (Dutton and Juday, 1944). Such a finding is not unreasonable if adequate free mixing can be postulated and both the absolute and relative amounts of pigments in plankton tend to be uniform within the euphotic zone (Marshall, 1956). By contrast littoral marine algae generally grow most abundantly at the particular depth where the spectral quality of the light suits their pigmentation (Levring, 1947; Blinks, 1955).

Earlier suggestions that the nature of the photosynthetic products depends upon the wavelength of light, that blue light favours protein formation and red light carbohydrate formation, has been disproved (Cayle and Emerson, 1957) but it is worth remembering that red light will be the most effective light, photosynthetically, for a given energy content. This has been remarked upon by several writers (e.g. Edmondson, 1956a) and it is obvious from the formulae in Section I of the present review that relate the number of quanta to the wavelength of light.

The varied pigment contents and the chromatic adaptability of a mixed marine phytoplankton population is such that, for all practical purposes, the only parameter that needs be measured in photosynthetic studies is the total radiant energy between 3800 and 7200 Å.

2. Energy Requirements

At relatively low light intensities the rate of photosynthesis by plants is a fairly linear function of the total radiant energy, i.e. the quantum efficiency is constant. As the illumination increases, however, less effective conversion occurs, due to a very rapid decrease in mean quantum efficiency (Barker, 1935; Jenkins, 1937; Nelson and Edmondson, 1955; Edmondson, 1956a; Ryther, 1956) which can overcompensate for any increase in illumination and result in a reduced gross production per unit time.

Ryther (1956), using his own ^{14}C data and the results on *Coscinodiscus* obtained by Miss Jenkins has divided the marine phytoplankton into three main groups, Chlorophyta, diatoms and dinoflagellates. The growth rate versus light intensity curves showed a linear increase up to 3×10^{-2} ly./min. in the first group, 7×10^{-2} ly./min. for the diatoms and 16×10^{-2} ly./min. for the dinoflag-

ellates. A subsequent increase of illumination then caused a continuous and almost linear decrease in production rate with the Chlorophyta. Photosynthesis was only a few percent of the maximum at 0.5 ly./min. The diatoms had a fairly constant production rate, between about 7 and 15 $\times 10^{-2}$ ly./min., but the rate then decreased rapidly and was again only a few percent of the maximum at 0.5 ly./min. The dinoflagellates, on the other hand, were more resistant and still photosynthesized at some 40 to 50% of their maximum rate when the radiant energy was 0.5 ly./min. Ryther (1956) gives a weighted average curve for the relative photosynthesis rate of temperate sea phytoplankton with light intensity. The results of other workers (cf. Meyers, 1946; Talling, 1955; Nielsen, 1937; Nielsen and Jensen, 1957) substantiate this behaviour but clearly the exact shape of the curve must vary according to the predominant species present in a mixed population and the geographic location. Results reported by Nielsen (1937) for temperature-zone water in autumn are very similar to the average values given by Ryther, but for tropical surface waters (Nielsen and Jensen, 1957) the population tolerates a greater light intensity and the curve lies to the right of even the dinoflagellate response curve determined by Ryther. However, the maximum growth of a mixed marine phytoplankton population can be expected where and when the radiant energy has a level near 0.15 ly./min. with a significant inhibition as the intensity rises to and exceeds 0.5 ly./min.

The detrimental effect of strong illumination on the photosynthetic mechanism is discussed by Nielsen (1952a). Subjecting plankton to inhibiting light intensities does not seem to reduce their viability when they are subsequently exposed to more suitable illumination, but the organisms will not adapt to these high intensities (Ryther, 1956). The most efficient utilization of light quanta is achieved by supplying the light in rapid bursts of about a millisecond duration with 10 milliseconds of darkness in between. Such a procedure can give a synthesis rate of up to 90% of that found with a continuous illumination. Under natural conditions intermittent illumination may occur near the surface, due to wave motion, and the ever-changing natural shading experienced in a dense plankton bloom in gentle motion is probably beneficial. Recent work by Cushing (1957) on the increased rate of ^{14}C uptake in bottles with one side darkened, compared to bottles more uniformly illuminated, may be related to light-intensity variations as plankton turn in an unequally illuminated environment. The highest quantum efficiencies recorded are around 20 to 25% but in most culture work the value appears to lie around 7 to 14% (Emerson and Lewis, 1943; Tanada, 1951; Yocum and Blinks, 1954; Blinks, 1955) and will doubtless depend on the physiological state of the plant, such as its reserves of adenosine triphosphate. The over-all conversion of radiant energy absorbed by the ocean into organic matter will clearly be much less efficient than this. Even if the conversion of light energy reaching the chloroplasts of marine plants is as high as in laboratory experiments (and it may not be), the amount of the total radiation that happens to strike plant tissue will be very low unless a dense bloom is present. In these circumstances an over-all efficiency of a few tenths of a percent is all that can be expected (Clarke, 1939). The effect of light polarization on photosynthetic

efficiency has recently been raised by McLeod (1957). The effect in nature may be significant.

The lower limit of light intensity for *gross* photosynthesis is probably, by definition, zero. The more practical minimum intensity limit, however, is the light necessary to maintain zero *net* synthesis, known as the "compensation intensity". At this intensity respiration and other metabolic losses are just compensated by photosynthetic processes and the mass of organic matter in the organisms stays sensibly constant. A difficulty of definition now arises. Over a short time interval of fairly constant illumination there will be a "steady state" compensation intensity sufficient to counterbalance respiratory losses and this intensity can well be expressed in ly./min. In nature, however, the plankton are subjected to a continually varied illumination intensity and, except in extreme latitudes, to no illumination at all during the night. Over a period of 24 hours (the most obvious time unit in this context) there will still be a mean level of radiant energy flux below which the plant will decrease in weight, but expression of this flux in ly./min., as is often done, is to be discouraged. There is no reason why the "steady state" and "24-hour" measures of compensation should be numerically the same and they most probably are not. The 24-hour value is the most realistic value for field work. It is therefore suggested that steady state compensation intensities be expressed in ly./min. but that the 24-hour value be recorded as ly./day or written as ly./min. (24-hour mean).

Either of these measures will be affected by factors such as temperature, nutrient availability and such physiological conditions of the phytoplankton that affect respiration. In mixed populations the recorded data, although apparently for phytoplankton, may be considerably different from the data for these plants alone, owing to the presence of zooplankton and bacteria. Therefore only approximate compensation values can be given which have but local significance or, at best, significance for seas of the same latitude and temperature. The "steady state" compensation intensity for pure cultures of *Chlorella* is probably about 1.5×10^{-3} ly./min. (quoted by Krauss, 1956) but the value given by Ryther (1956) for phytoplankton lies around 3 to 6×10^{-3} ly./min. Schomer and Juday (1935) for cultures from lakes which were not bacteria-free found a mean of about 7×10^{-3} ly./min.(24-hour mean). Jenkins (1937) for cultures of *Coscinodiscus excentricus* in the English Channel records 2.1×10^{-3} ly./min. (24-hour mean), but quotes a figure by Schrieber of a quarter of this for *Biddelphia mobiliensis*. Pettersson, Hoglund and Landberg (1934) found, for a mixed population containing zooplankton, a value of about 2.4×10^{-3} ly./min. (24-hour mean) but later revised this to make it some 25% higher (Pettersson, 1938). There is evidence that the quantum efficiency of photosynthesis increases at very low light intensities (Kok, 1951) and possibly a self-regulatory mechanism enables a plant to compensate over quite a range of intensities. The best that can be said at present is that the 24-hour mean figure for phytoplankton populations, not excessively contaminated with other microflora or fauna, centres around 3×10^{-3} ly./min. (24-hour mean) or some 5 ly./day in temperature seas. The compensation intensity is bound to increase with increasing

temperature and the whole subject of the interdependence of light and temperature in photosynthesis merits some discussion.

3. Temperature and Light

If the rate of gross photosynthesis were independent of temperature the net rate of production of organic matter at a given light intensity would be an inverse function of temperature, owing to the positive effect of temperature on the respiration rate. This may in fact occur to a significant extent (Levring, 1947). It is unlikely that the respiration of a plant is greatly affected by simultaneous photosynthesis, although it may decrease somewhat during the exponential stage of vigorous reproduction (Ryther, 1955). The temperature dependence of photosynthesis cannot always be neglected, however, and it is a complex function of light intensity, generally increasing with the degree of illumination to which the plant is subjected.

Thus Wassinck and Kersten (1944) found practically no temperature coefficient at illuminations of 3×10^{-2} ly./min. or less for the diatom *Nitzchia dissipata* but quite a large effect (below 10°C.) when the light intensity was about twice this amount. The rate of reproduction of diatoms subjected to saturation light intensities had a Q_{10} value of 2 between 8 and 18°C. (Spencer, 1954). Barker (1935) found similar results for photosynthetic production (*N. closterium* and *N. palea*), there being a smaller coefficient at low and high temperatures. Talling (1955) reported a Q_{10} value of 2.3 between about 5 and 16°C. for the fresh water *Asterionella* at saturation light intensities; see also Printz (1939) and Ehrke (1931). Riley (1956) reports a positive temperature coefficient for *Skeletonema* but the reverse effect for *Thalassiosira*. The ^{14}C uptake of a mixed surface population doubled in rate between 5 and 10°C. but increased only a further 40% between 10 and 15°C. (Wimpenny, 1957).

The underlying causes of this complex behaviour are well established in principle. With adequate carbon dioxide and nutrients, and only weak illumination or scant pigmentation, the governing rate is that of the primary photochemical process which has little or no temperature dependence ($Q_{10} \rightarrow 1$). If the carbon dioxide or nutrient concentrations are very low, however, the rate-determining step at any illumination may be that of the transport of these substances up to and within the plant cells and this will have a Q_{10} value around 1.3. Only when both light and nutrients are in excess will the enzymatic, non-photochemical processes assume control and the overall synthesis have the high Q_{10} value (greater than 2) characteristic of such reactions. Available data are summarized by Rabinowitch (1956, p. 1236) and in many cases the Arrhenius Law is valid over about 10-degree C. temperature ranges, with activation energy values between 10 and 30 kilocalories. Before either extreme in the biokinetic temperature range is reached, the Arrhenius equation breaks down with the apparent activation energy values decreasing.

The behaviour varies greatly from species to species and it is difficult to generalize. As Nielsen (1955) has pointed out, great adaptation is possible and this will tend to even out differences in behaviour from ocean to ocean, although for any given latitude temperature variations will have a similar relative effect.

The net synthesis by marine plants, even under strong illumination, will most likely decrease at the higher sea temperatures because of the fact that the gross photosynthesis curve commences to flatten above a certain temperature whereas respiration continues to increase exponentially (Rabinowitch, 1956). Under conditions where much of the euphotic column is subjected to sub-optimal intensities, as in early spring and late autumn, the negative temperature coefficient of net synthesis will be most marked and may well be a contributing factor to the relative size of spring and autumn plankton blooms. The latter will occur in waters some 10 degrees C. or more warmer than found in early spring.

It is clear that neither the Arrhenius equation, nor more complex equations that assume a combination of several temperature dependent processes, will yet predict the photosynthetic rate over a wide range of temperature and illumination for even one species of plant. A resort to purely empirical equations, applicable to a limiting range of conditions, may have some value but there is a great danger that such a practice may lead to unjustified extensions and extrapolations in the field.

For example, the equation given by Baly (1935) relating photo-synthesis to temperature and light intensity has been used by Riley, Stommel and Bumpus (1949) despite the fact that it is now known to have no valid theoretical foundation. The form of the equation was such that it gave a reasonable fit to some of Emerson's early data on *Chlorella* when constants were determined empirically. There seems little justification, however, in applying it to a mixed population under a wide range of illumination conditions. Only the logarithmic form of the equation, the limited range of light intensities considered and the broad limits of precision accepted as adequate by ecologists can account for its apparent success. Other empirical functions might well be as suitable. Less exception can be taken to using more simple relationships (Riley, 1946, 1947; Edmondson, 1956b; Verduin, 1956) where the production rate is assumed proportional to the surface illumination, or to an integrated mean intensity within the euphotic zone. Much of the production may well be under conditions where there is little direct temperature effect or where the temperature is sufficiently constant to be neglected to a first approximation.

VISION AND STIMULATION BY LIGHT

As well as providing the primary energy source for food production in the ocean by photosynthetic processes, light has significance in productivity studies because it acts as one of the stimuli affecting the grazing habits of zooplankton and assists fishes and other marine organisms in discriminatory feeding.

Certain of the phytoplankton would appear to be positively phototactic. Pomeroy, Haskin and Ragotzkie (1956) have recently described the swarming of dinoflagellates to the surface where they tend to be concentrated at weak convergences. The diurnal migration of much of the zooplankton population is well known (for example, Nicholls, 1933; Waterman *et al.*, 1939). The effect depends on the sex and physiological state of the plankton and some of the

migration may be independent of light stimulus (Esterly, 1917). The movement up into the euphotic zone occurs soon after sunset and a return to greater depths commences at, or even before, the dawn. Clarke (1934) considered all the factors that might effect this migration and concluded that the movement (at a rate of up to 1.3 m./min.) could only be caused by gravity, light and possibly the presence of other organisms. Clarke (1933) also noted the difference in behaviour of different species and remarked that the adult female *Metridia*, which exhibited the most marked movement, never entered water where the illumination exceeded about 10^{-2} ly./min. The subject is well reviewed by Cushing (1951) and has recently been studied in the laboratory (Harris and Wolfe, 1956).

The idea that the zooplankton congregate at a definite light intensity and migrate so as to keep in water having this critical illumination was implied by Waterman *et al.* (1939) and is substantiated by the findings of Kampa and Boden (1954) who reported the critical intensity off the coast of California to be 1.5×10^{-8} ly./min. This compares with a value of 14×10^{-8} ly./min. found in the Atlantic by Clarke and Backus (1956) for the illumination of the zooplankton layer at its maximum depth (mid-day). In the California work the light was measured in a horizontal direction, whereas in the Atlantic Clarke and Backus had their photometer pointing vertically upwards. This would tend to make the agreement between the two data considerably better. However, Clarke and Backus reported that at sunset their scatter layer rose into water irradiated with some ten times this energy, so factors other than the pursuit of a given intensity of light may well be involved in these diurnal migrations. W. H. Johnson (1938) had suggested earlier that for *Acartia clausi*, at any rate, the organism required a change in intensity to evoke vertical migration and that the more rapidly or frequently the change occurred the more the animal was stimulated, moving towards light after having been in "darkness" and away from light if the light increased after the animal had adapted to a given intensity.

Generalizations are difficult at present but it would seem reasonable to say that a significant fraction of the migratory zooplankton concentrates where the light intensity is about 10^{-7} ly./min., measured vertically, and is much less at intensities differing from this by a few orders of magnitude. Many species in the zooplankton, however, appear to have little or no orientation to the light intensity. The positive response of living creatures to polarized light has been established terrestrially, but only comparatively recently has the potential importance of such a response in submarine fauna been fully realized (cf. Waterman, 1955; Waterman and Westell, 1956; Bainbridge and Waterman, 1957.)

Recent work with sonic recorders has shown that the "deep scatter layer" associated with plankton usually separates into two layers durings its vertical movements and there can be little doubt that the layer consists of light-sensitive migrants together with an associated population of predators. The lower of the two layers formed after separating was found by Kampa and Boden (1954) to be of a low-frequency scattering type suggestive of fish which, presumably, must have been capable of sighting their prey at an illumination of 10^{-7} ly./min. Much of the speculation on the lower limit of light intensity for fish vision stems

from the observations on *Lepomis* by Grundfast (1932) which suggested that the intensity limits for vision were similar to those for the human eye, about 10^{-10} of full sunlight or of the order of 5×10^{-11} ly./min. at 5000 Å. There is no reason to assume that this is the lower limit for all submarine life as adaptation by fish habitually frequenting great depths would probably increase their sensitivity. The limit of visual intensity is not necessarily the optimum of desirable limit of illumination for a fish. For discriminatory feeders the intensity would need to be considerably higher and Brett (1957) reports this limit for Pacific salmon to be of the order of 10^{-9} ly./min. There can be little doubt that the fish would normally feed where the illumination was much greater and a knowledge of the intensity limit is only useful in deciding the depth below which it is unreasonable to expect to find an actively feeding population (Clarke, 1936a, 1936b).

Section III: Observed Distribution of Radiant Energy

ENERGY AT THE OCEAN SURFACE

The radiant energy spectrum of the sun approximates to that of a black body at 6000°K, although giving significantly less radiation between 3000 and 1000 Å and rather more below 1000 Å. The total amount below 2000 Å is probably small and a range of 2000 to 30,000 Å is generally considered to cover the effective wavelengths.

1. Amounts and Variation

The solar constant is a measure of the amount of energy reaching a plane surface 1 cm.^{2} in area placed perpendicular to the sun's rays outside the earth's atmosphere. The value for this constant is still not known with great accuracy but probably lies between 1.90 and 1.94 ly./min. and does not exceed 2 ly./min. The subject is well reviewed by Fritz (1951) who gives a graphical record of the mean 24-hour values of the radiation reaching a plane *parallel* to the earth's surface, but outside the atmosphere. The amount of radiant energy reaches a mean of 1100 ly./day at the poles during summer and between 800 and 900 ly./day at the equator at the time of the equinox.

On penetrating the atmosphere, energy is lost due to scattering and absorption by such molecules as water, carbon dioxide and ozone. Oxygen and nitrogen have relatively little effect. The absorbed radiation reappears as very long-wave heat radiation (exceeding 50,000 Å) which is derived from the kinetic energy of water and other molecules (cf. Moller, 1951). Although of the order of several tenths of a langley at the earth's surface, this radiation has only recently been measured by direct methods during the day (cf. Anderson, 1952) using instruments such as the Gier and Dunkle radiometer (Gier and Dunkle, 1951). As far as is known it has no direct bearing on productivity or biological studies.

The radiant energy reaching the ocean surface is no longer a simple function of the sun's angle but depends on such factors as the cloud cover and the dust and water vapour content of the atmosphere. Mean daily values for this radiation at various parts of the world, in particular the United States of America, have

been collected (e.g. Kimball, 1928; Hand, 1941) and Edmondson (1956a) gives a fairly complete bibliography. Atkins (1938) reported seven-year mean values at Plymouth. Kimball evaluated the mean daily totals for the twenty-first day of each month at some two dozen stations around the globe, assuming a cloudless sky but taking into account the atmospheric moisture for each area. The latter varies but little over the oceans at a given latitude. The relationship between the mean value for a cloudless day and a cloudy day was taken as:

$$\bar{I} = \bar{I}_0(1 - 0.71\,c) \qquad (1)$$

where $\bar{I}_0$ was the radiation received under cloudless conditions and $\bar{c}$ the mean proportion of cloud cover for a given location. Values for $\bar{I}_0$ over the ocean at 48°N. were at a maximum in June at 805 ly./day, and a minimum in December at 160 ly./day. An illustration of the effect of cloud is given by the fact that the maximum for $\bar{I}$ near the south end of Vancouver Island was only 414 ly./day (in May, not June) and the minimum (in December) was only 71 ly./day. At latitude 48°N. the radiation at the ocean surface will rarely exceed 1.5 ly./min. although transient values as high as 2 ly./min. may be possible with the right cloud conditions (Fritz, quoted by Edmondson, 1956a). The vertical illumination at sunset and sunrise is only a few percent of the daily maximum and even with full moonlight the night illumination does not exceed about 10^{-7} ly./min. and can be neglected. If the weather conditions remain constant a rough 24-hour mean intensity at latitude 50°N. in the summer or winter can be taken as 0.4 times the value at noon. This 24-hour mean figure has a *maximum* of about 0.55 ly./min. in June and 0.11 ly./min. in December. The *average values* are 0.28 ly./min. and 0.04 ly./min. respectively. However, hourly and daily variations are so extreme that there is no substitute for making an integrated direct measurement, experimentally, at any locality if detailed productivity or meteorological studies are contemplated. Equation (1) only applies to mean values taken over several weeks.

2. Spectral Distribution

There is little or no direct solar radiation with a wavelength less than 3000 or exceeding 50,000 Å, the upper limit measured by most pyrheliometers. It is important to know the relative amounts of energy between given wavelengths in order to decide what fraction of the total incident radiation is photosynthetically active and what fractions lie in the various wavebands in the visible portion, as these penetrate into the ocean to various extents.

The fraction of the total radiation received at the ocean surface which is in the photosynthetic range 3800 to 7200 Å will vary with the atmospheric conditions and height of the sun but a value of 0.5 is sufficiently precise for field work of several days duration (see Section I; Atkins and Poole, 1936a, and the discussion by Edmondson, 1956a). The worst errors will arise when a cloud obscures the sun in an otherwise clear sky, or at morning and evening when the sun's angle decreased below some 20° to the horizon. In the latter instance the factor may drop to as low as 0.35 to 0.4.

The spectral distribution in direct sunlight varies with sun angle and the amount of water vapour and dust in the atmosphere. Useful computations will be found in the Smithsonian Tables (List, 1951; Forsythe, 1954). The distribution in blue sky is significantly different from that of the sun (Atkins and Poole, 1931), and if measurements are made with a horizontal photometer on a clear sunny day account must be taken of the relative contributions of sky and sun as has been done in Section I (Atkins and Poole, 1936b; Jenkins, 1937). A most useful set of curves from the work of Taylor and Kerr is quoted by Rabinowitch (1951). These show the relative spectral distribution of daylight from various sources, sun, sky, overcast, etc. The sun-plus-sky light on a horizontal plane is very similar to the light from total overcast but the zenith or northern sky light alone has a much larger contribution from short wavelength radiation and less from wavelengths exceeding 5600 Å. The relative spectral distribution of energy in a cloudless sky is given between 3500 and 7500 Å as a function of sun's altitude by Johnson and Kullenberg (1946) quoting data from Albrecht (1936) and Kimball (1924) (see Table II). Jerlov (1954) presents a list of filter combinations to simulate the spectral characteristics of a blue sky plus sun when an incandescent lamp is used as light source.

TABLE II. Relative spectral distribution of daylight energy for a cloudless day.

Wavelength (Ångstroms)	Solar altitude		
	15°	35°	65°
3500	0.056	0.117	0.456
3750	0.103	0.439	0.564
4000	0.183	0.732	0.736
4250	0.306	0.866	0.868
4500	0.429	0.966	0.959
4750	0.619	1.000	1.000
5000	0.782	0.995	0.990
5250	0.877	0.983	0.942
5500	0.933	0.966	0.904
5750	0.980	0.937	0.890
6000	1.000	0.907	0.882
6250	0.980	0.849	0.849
6500	0.940	0.790	0.825
6750	0.947	0.754	0.806
7000	0.980	0.732	0.763
7250	0.952	0.720	0.715
7500	0.952	0.702	0.664

LOSSES AT AND IN THE OCEAN SURFACE

An appreciable fraction of the radiant energy reaching the ocean surface does not penetrate into the water and losses occur by true reflection, by back scattering from particles near the surface and, reputedly, by a third loss mechanism which is not yet completely understood.

Poole and Atkins (1928), Atkins and Poole (1933) and others take a mean value of 15% for the total losses, which is probably a good enough estimate for field work, where a long-term average of radiant energy is being measured. The actual value will vary considerably from moment to moment, however, varying

with the conditions of the sea surface and the cloud cover. On a fine day in summer the loss will be only a few percent under conditions of glassy calm and will increase to 5–17% with light winds and to over 30% for moderate to strong winds.

The component of this loss corresponding to true reflectivity is generally not very great. For an overcast sky the value averages 6 to 7% (Powell and Clarke, 1936) but this value is considered low by Nieburger (1948) and the true value may be near 10%. For direct solar radiation the loss is less than 3 or 4% unless the sun is below 30°, when the reflectivity climbs rapidly, being over 25% at a sun angle of 10°. A compilation of values for the sun in a clear sky is given by Sverdrup *et al.* (1942) and a modern review of theory and practice, with special reference to energy budget studies, will be found in the article by Anderson (1952).

Powell and Clarke (1936) showed that the amounts of reflected and back-scattered light were approximately equal and not only smaller than once supposed, but little dependent on the wavelength of light or on the degree of surface roughness of the ocean. There was a slight increase for whitecaps and rough sea but even over the wake of a motor-boat the total loss reached only 12%. On measuring the actual amount of light penetrating the water below a few metres, however, it became obvious that the total loss of radiation in the surface layer was much higher than would be expected from the reflection and back-scattering data alone and reached a value of over 30% in rough weather. The explanation for this third form of "surface loss", which depends so much on the roughness of the sea, is not clear. Powell and Clarke suggested that the loss was due to scattering and multiple internal reflections in the layer of bubbles which is always found in the top few feet of water when the ocean surface is disturbed. Poole (1938) was mildly critical of this explanation, pointing out that the size of these bubbles would be too great for them to contribute significant true scattering. He suggested that an explanation might lie in the fact that the surface bubbles greatly increased the obliquity of the radiation trapped in the upper layer, which showed up as a marked increase in vertical extinction coefficients, but he considered the effect to be surprisingly large.

ABSORPTION AND SCATTERING WITHIN THE OCEAN

1. Absorption and Scatter under Ideal Conditions

The absorption of light in pure water is so small, except at extreme wavelengths, that considerable experimental difficulties are encountered in its measurement and there is not exact agreement between the results of various workers.

True absorption occurs in the infrared, and the Lambert Law constant (see Section I) is already around 20 at 10,000 Å and rises rapidly with increasing wavelength. For all practical purposes, energy of wavelengths exceeding 10,000 Å is completely absorbed in the first 10 cm. of the ocean surface and 2 m. of water ensures the removal of energy beyond the visible or photosynthetic range. Appreciable absorption at the red end of the spectrum can be detected at 5000 Å.

Below this wavelength water is very transparent and there is probably little true absorption until the far ultraviolet. The process of molecular scattering by the water, however, makes the effective κ° values increase appreciably below about 3500 Å but there are few data available for this region and results are conflicting. The values of κ° below about 5000 Å become increasingly susceptible to the presence of particulate matter. Particles of less than one micron in diameter (10,000 Å) can have very marked effects at wavelengths below 3500 Å and the extinction values quoted by Sverdrup *et al.* (1942) in this region are probably high. Although the true κ° value at 3000 Å may only be one or two tenths of a unit or less, the presence of a minute amount of solid material in suspension completely alters the picture by causing short wavelength scattering and it is the occurrence of such Rayleigh scattering that is, in practice, responsible for much of the attenuation of short-wave illumination in water. The subject is treated in standard physics texts; see also Burt (1955a). Suspended material, unless it is excessive, has relatively little effect at wavelengths exceeding 6000 Å as it then acts mainly by direct blocking of the light rays. Absorption due to the anions and cations of dissolved salts in the ocean is not significant at wavelengths greater than 3400 Å (Lenoble, 1956b), but the traces of organic matter present in most natural waters, even when they are filtered, tend to increase κ° values in the blue and ultraviolet (Burt, 1953; see also Table III). The main source of absorption from organic matter is the so-called "yellow substance" found to a greater or less extent in all coastal waters. Its nature is still uncertain but the substance or substances are probably stable oxidation products of marine or terrestrial plant life (Jerlov, 1953, 1957; Kalle, 1938, 1949).

In pure water there is no wavelength of maximum transmission, only a very broad maximum from about 3900 to 5500 Å. With clear natural waters, as found in the open ocean, the peak transmission is ill defined but it is in the blue, near 4800 Å. For turbid inshore waters a more pronounced maximum is found at 5500 Å and with very turbid brown-coloured lakes the maximum may even be in the yellow or orange part of the spectrum.

In Table III a few averaged values for κ° have been calculated from the data of Clarke and James (1939) which illustrate the general behaviour of pure and natural waters.

TABLE III. κ° values for various types of water calculated from the data of Clarke and James, 1929.

Wavelength (Ångstroms)	Pure water	Filtered coastal water	Open ocean water	Coastal water, moderately turbid
8000	0.885	0.84	0.865	1.01
7600	1.11	1.10	1.13	1.25
7000	0.215	0.22	0.265	0.40
6300	0.10	0.095	0.14	0.31
5800	0.05	0.05	0.07	0.32
5500	0.03	0.025	0.045	0.32
5000	0.015	0.014	0.04	0.33
4700	0.007	0.012	0.04	0.35
4000	0.016	0.045	0.055	0.50
3600	0.02	0.08	0.065	0.65

In a review by Clarke (1939) the spectrum of sunlight at the surface and at various depths in pure water is given, the graph being taken from data by Birge and James. This graph gives an excellent illustration of the combined effect of solar emission and water absorption. The wavelength of maximum penetration is again close to 4800 Å but the rapid decrease at shorter wavelengths arises mainly from the distribution of light in the initial solar spectrum rather than from absorption effects.

2. Attenuation under Natural Conditions, Vertical Extinction Coefficients

The observed penetration of light into the ocean follows a much more complex pattern than that indicated by the above discussion for pure and turbid waters. Radiation from the sun rarely has zero angle of incidence and much of the light striking the ocean surface will be from sky or clouds and be diffuse, entering at all angles. The light scattered by particles in the sea is not lost by the system (as would be the case in a spectro-photometer tube) and its subsequent distribution must be considered.

If we neglect sky radiation, the incident sunlight on a smooth sea surface penetrates vertically only when the sun is at its zenith. Whitney (1938a) considered the problem in detail and introduced the term "path length" which is the mean distance the light must penetrate to reach a metre in vertical depth. This distance follows from simple optics and has a minimum of 100 cm. at zero zenith angle and exceeds 150 cm. when the sun is below 10° to the horizon. For diffuse sky radiation the problem is more complex but was solved graphically by Whitney who published a diagram showing mean path length values for various sun angles and percentages of sky radiation. For total overcast the length is 118 cm. and independent of the sun's angle.

For experimental simplicity and to obtain illumination values of practical significance Atkins and Poole (1933) suggested that when the attenuation of light with depth is measured by photometers looking vertically upwards the constants for the Lambert Law obtained by this mean be termed vertical coefficients (k and κ). This practice is now universal, and most of the extinction coefficients reported in the oceanographic literature are of this form, although it is sometimes difficult to decide whether k, κ, κ°, or k° figures are being quoted. As Utterback and Jorgensen (1934) pointed out, the Lambert Law applies strictly to vertical parallel light and for oceanographic work should be of a form:

$$I_\lambda = I_{0\lambda} e^{-k^\circ z (\sec r)} \qquad (2)$$

where sec r is the secant of the angle of refraction, r, of the beam in water. Vertical extinction coefficients take no account of r or of the scattering components of light attenuation. With monochromatic light in a particle-free column of water κ changes with depth due to the amount of oblique light becoming steadily less (Poole, 1936; see Section I for the relation between κ, κ° and path length at the sea surface). With particulate matter present the average obliquity of light rays with depth is largely governed by absorption, which filters out the

more oblique rays, and scattering, which increases the obliquity of the remaining rays. Eventually the initial angle of surface illumination or the conditions of the ocean surface play a minor role in the distribution of submarine light (Atkins and Poole, 1933). Evidence suggests that the mean altitude of the sunlight remaining at 10 to 20 m. is 50 to 60° (Poole and Atkins, 1928; Atkins and Poole, 1940).

3. Scatter and the Angular Distribution of Submarine Light

The combined effects of absorption and scattering on the obliquity of submarine light result in an equilibrium state at sufficient depth and from thence downwards the ratio of the illumination from any two directions is constant (cf. Whitney, 1938b). Utterback (1936) measured the ratio of the back-scattered light (photometer looking downwards) to vertical illumination at various depths in the Pacific for various wavelengths of light. The ratio increased with depth but was fairly constant, between 2 and 3%, at 25 m. The ratio has been measured by Jorgensen and Utterback (1939), Atkins and Poole (1940), Jerlov (1947a) and Lenoble (1956b, c), to name but a few, and increases with decreasing wavelength to a value of 7% or greater at 3300 Å. The ratio of horizontal to vertical illumination is greater than the back-scattered to vertical ratio, being of the order of 10 to 20% in the visible part of the spectrum (Poole and Atkins, 1928; Clarke, 1936b; Pettersson, 1938; Whitney, 1938b, 1941; Jerlov, 1947a; Lenoble, 1956b, c). Pettersson (1938), Johnson and Liljequist (1938) and Jerlov (1947a), amongst others, have made several measurements of the angular distribution of submarine light and a detailed treatment will be found in these papers and in the papers by Whitney (1938b, 1941) who extended his "path length" concept for the correlation of κ and κ° to cover the effects of submarine scattering.

The scattering of light in purified waters has been studied extensively by Atkins and Poole (1940, 1952, 1954). Blue light is scattered more than red and green light, the difference between the last two being scarcely significant. Filtration through a 0.1 micron pore-size filter increases the difference between blue light and the light of other colours. Lenoble (1956a) has shown that the scattering is not isotropic but has the forward component to be expected from relatively large transparent particles (plants, detritus, sand grains) (cf. also Atkins and Poole, 1952). The nature of the suspended matter in the sea is discussed by Atkins, Jenkins and Warren (1954) and by Armstrong and Atkins (1950).

The total extinction coefficient of natural waters may be considered to be the sum of three separate coefficients, the "persistent" coefficient for pure water itself, the coefficient arising from the absorption by suspended particles and dissolved substances and the scattering coefficient arising from suspended particles. The "persistent" coefficient for pure water results from true absorption and a scatter component which increases rapidly at short wavelengths (Le Grand, 1939). The scatter from particulate matter is only slightly selective to light of different wavelengths in tropical seas (Jerlov, 1947a). Lenoble (1956b) has treated the subject of the observed angular distribution of light and vertical

extinction coefficients in a mathematical theory based on scatter and absorption (see also Jerlov, 1947a). The intense blue colour of a tropical sea is explained on the grounds of the selective absorption of red light and the selective scatter of blue light which predominates in upward scattered light (Jerlov, 1947a; Lenoble, 1956d).

The variation of turbidity and scattering with depth and with location has been studied by Pettersson (1934, 1935), Oster and Clarke (1935), Burt (1955b), Jones and Wills (1956) and Young (1939), amongst others. Jerlov (1947b) made extensive studies in oceanic and inshore waters using a very sensitive laboratory instrument. There is not only an increase in suspended matter in going from the open ocean to inshore waters but the latter often have high concentrations of such matter at the surface and in thin strata near the thermo or haloclines. The relation between κ° values and the number of mg./litre of suspended solids has been studied by Jones and Wills (1956) and is nearly linear with up to 10 mg./litre. Values for κ° as high as 0.9 were recorded in the narrow bands of high turbidity found at the halocline off the Scandinavian coast and in river estuaries. In deeper layers values do not exceed 0.15 and in offshore waters may be much less than 0.05.

Deep waters are nearly always less turbid than the upper layers but sometimes zones of low turbidity can occur at 30 to 40 m. (Young, 1939). Curves showing the transparency and scattering of turbid water with depth are often beautifully anti-symmetrical (maximum scatter for minimum transparency) and bands of high turbidity are easily revealed.

An important consequence of the obliquity of radiation found at depth in the sea is that the total illumination received by a plant in the euphotic zone will be considerably more than the value measured by a photocell facing upwards, which is the normal measurement taken. The ratio of total to vertical illumination has been measured by Pettersson (1938) and depends both on the meteorological conditions and the turbidity of the water. In the first 5 to 10 m. this ratio may be as high as 1.5 on a clear day with turbid water. A value of 1.2 to 1.3 for the whole euphotic zone is not unreasonable (Jerlov, 1947a).

The quantitative study of the linear polarization of submarine light is comparatively recent and is well described by Ivanoff (1957), Waterman (1955) and Waterman and Westell (1956). At depths, the polarization is mostly in a horizontal plane at right angles to the direction of the sunlight in the sea. The fractional polarization is highest in clear water and the technique may prove to be a more sensitive indicator of water masses than either turbidity of scatter measurements.

4. Data on Vertical Extinction Coefficients

Oceanographic data on the penetration of submarine radiation are usually expressed as vertical absorption coefficients. The spectral change of light with depth is of the nature predicted by Table I. All the red light has gone in the first 5 to 15 m. and blue light penetrates most in clear waters. In turbid areas

green light has the greatest penetration. A general idea of these spectral changes with depth can be obtained from Miss Jenkin's paper (1937) and from the monograph by Clarke (1939).

For reasons discussed above, vertical coefficients are smaller than would be expected from the κ° values in Table III and even with monochromatic light and a homogeneous water mass there is a decrease of κ with depth down to some 25 to 50 m. Jerlov (1947a) has reported the light attenuation curves for light of various wavelengths at numerous stations, mostly in clear tropical waters. κ values are almost invariably greater in the top 50 to 70 m. than in the succeeding 100 m., especially for blue and green light. The effect is greatest where there is high scattering in comparison with absorption, and with water of appreciable absorptive powers ("yellow substance" present) a much more uniform κ value is found after the first few metres.

From the recent work of Kampa (1955) in the San Diego Trench, and of Clarke and Wertheim (1956) off Miami, it would appear that water below 100 to 200 m. is uniformly clear with a κ value for green light (the only spectral range present to any significant extent) of around 0.015. As Kampa has pointed out, the presence of this clear water makes it impossible to extrapolate with any certainty light intensity values measured in the top 25 to 50 m.

This variation, and the changes of κ that occur if the water column is not homogeneous, underline the undesirability of reporting "average" κ values, although this is often attempted. As with surface radiation measurements, there is no substitute for field observations if quantitative productivity studies are to be made. The main disadvantage in measuring κ is that the work can only be carried out at any reasonable depth during the hours of bright daylight (cf. Atkins, Clarke *et al.*, 1938) and, even then, photomultipliers have to be used for depths exceeding 100 to 200 m.

A bibliography of world coverage will not be attempted in this review as it serves little useful purpose. The following summarizes many of the better known investigations made in the oceans off the North American continent, which are doubtless representative of most other areas (cf. for example, Poole and Atkins, 1937; Sasaki *et al.*, 1955).

Pacific ocean. The pioneer work in this area was by Utterback and his school. In 1933 Utterback (1933a) studied the waters off southern Alaska and the coastal inlets. The water was more turbid than that around the San Juan Archipelago studied the same year (Utterback and Boyle, 1933). In 1934 Utterback and Jorgensen published a very thorough study of the Pacific between 47° and 49°N. and from Vancouver Island and the Olympic Peninsula out to 130° W. Depths up to 72.5 m. were investigated using seven wavebands of light. Mention should be made of the investigations in waters adjacent to Vancouver Island, again for seven wavebands and to depths of 70 m. Some time studies were made in this area, there being a maximum turbidity recorded in June and a minimum in December. A series of papers covers observations from 1935 to 1939 (Williams and Utterback 1935; Utterback 1936; Utterback and

Jorgensen 1936; Utterback and Miller 1937; and Jorgensen and Utterback 1939).

ATLANTIC OCEAN. In this area Clarke and co-workers have made numerous surveys. In 1935 Oster and Clarke determined κ values at many stations in the Atlantic. κ values increased progressively going from the Gulf Stream to Woods Hole Harbor. Clarke (1936b) made a further study of the Sargasso area (one of the most transparent oceans of the world), the Gulf of Maine and stations inshore to the harbor at Woods Hole. A further collection of Atlantic data off Woods Hole is given by Clarke (1938) and Clarke and Oster (1934). Light penetration into the Caribbean and Gulf of Mexico is described by Clarke (1937).

As a *rough guide* to the magnitudes involved, approximate values for κ are suggested in Table IV. They will only serve to predict the order of magnitude of light attenuation, but this may be of some help in the design of experiments in oceanic biology and productivity.

TABLE IV. Suggested approximate κ values for various types of water.

Location	κ values		
	Red light 6000–7000 Å	Green light 5000–5800 Å	Blue light 4000–4800 Å
All waters below about 100 m.	0.15	0.015	0.025
Clear oceanic water, upper 50 m.	0.15	0.03	0.04
Moderately turbid inshore waters, upper 25 m.	0.2	0.08	0.12
Very turbid inshore waters, upper 10 m.	0.35	0.2	0.25

CALCULATIONS INVOLVING VERTICAL EXTINCTION COEFFICIENTS

As the vertical extinction coefficient appears in the exponent of the Lambert Law, *submarine illumination at depths exceeding a few metres* will be a more sensitive function of κ values than of the intensity of surface illumination. For example, throughout the year, Clarke (1938) found the illumination at 30 m. changed by as much as four orders of magnitude, mostly due to changes of κ. If the average value of κ were to double, the illumination at 100 m. might be reduced to much less than one thousandth of its previous value. The effect at even 10 to 20 m. in most waters would be greater than any daily variation of mid-day illumination at the surface.

The *depth at which a given illumination occurs* is not so sensitive a function of κ, because the depth term in the Lambert Law is in the exponent. Nevertheless a percentage change in κ will show up as a proportional change in this depth. On the other hand changes of surface illumination often have little influence because the change in the depth for a given illumination is a function of the logarithm of the surface light intensity. For a κ value of 0.1, a ten-fold decrease in the

surface light would decrease the depth at which a given illumination is found by 10 m., an amount which is negligible at great depths.

If the κ values for green light average at κ_1 to a depth d_1, and thence κ_2 for a further distance d_2, etc., then:

$$\kappa_1.d_1 + \kappa_2.d_2 + \ldots \kappa_n.d_n = \log I_s - \log I \qquad (3)$$

where I_s is the surface illumination in the green region of the spectrum, (say 0.12 ly./min.$_T$, see Section I) and I is the illumination at the depth which concerns us. If κ values are known the total depth $d_1 + d_2 + \ldots d_n$ can readily be calculated. For the limit of fish vision we can put log I equal to -10.3; for the limit of discriminatory feeding, equal to -9; for the migratory zooplankton equal to -7; etc. Mean I_s values will depend on the time of day and year or can be experimentally determined.

The maximum depth for fish vision has been calculated by Clarke, making the approximate assumption of a constant κ value (Clarke, 1936b; 1939). The general order is 75 m. in turbid inshore waters, 150 m. in slope waters and 450 m. in the clearest part of the ocean.

If κ values are known it is easy to calculate the illumination at any depth as a fraction of the surface illumination by direct application of the Lambert Law. An assumption of constant κ values with depth is often made but this is not necessary if the variations of κ with depth have been determined, as a graphical evaluation is straightforward. No extrapolation should be attempted, however, until a depth of 100 m. or more is reached.

For an accurate prediction of the *total amount of radiant energy present in the water down to a given depth*, κ values must be known for at least three wavebands (as in Table IV), preferably more, and the distribution of solar energy in the spectrum at the surface has to be considered. It is then a simple matter to construct mean energy curves for each spectral band, commencing at zero depth with a point on the illumination axis corresponding to the correct solar energy, and finally summating and integrating the values graphically (see for example Jenkins, 1937).

The *compensation depth of the euphotic zone* is generally such that all red light and some of the blue light will have been absorbed. The κ value for green light, a value of 0.15 ly./min.$_T$ for I_s and a value of -2.7 for log I can therefore be used in equation (3) to predict the compensation depth, but the result will be very approximate. Clarke (1939) in his monograph computed the compensation depth within the Sargasso Sea to be greater than 100 m., in the English Channel some 45 m., 24 to 30 m. in the Gulf of Maine and 7 m. at Woods Hole Harbor. He quoted Marshall and Orr (1928) for the statement that the maximum depth of fixed plants is 130 to 160 m. in the Mediterranean, 50 m. off Iceland and 20 m. in the Baltic. Neilsen (1955) gave the compensation depth as 95 to 120 m. in the tropics and 75 to 85 m. in the Equatorial Counter Current. Such values serve merely as intelligent guesses and should be treated with reserve. For any field experiment the depth will be in the range obtained by calculating the length of water columns necessary to reduce the flux to between say 2×10^{-3} and 5

$\times 10^{-3}$ ly./min. (24-hour mean) using the summation of energy values at the various wavelengths and the 24-hour mean ly./min. of radiation at the surface. The steady state compensation depth at midday will be below the 24-hour mean depth but only some 4 to 5 m. lower in most waters.

A knowledge of the *total amount of radiant energy below unit area* of the euphotic zone may be useful for productivity studies and is proportional to the integral of flux with depth. (For dimensional correctness the flux should be divided by a velocity term.)

We may write:

$$Z_d = \frac{I_s(1 - 10^{-\kappa_\lambda d})}{2.3\kappa_\lambda} \tag{4}$$

where d is the compensation depth. In effect, this expression defines a depth of water in which a suitable range of intensities for photosynthesis will be found.

If the simplifying assumption is made that productivity everywhere within the zone is proportional to energy, a measure of productivity is obtained by multiplying Z_d by a suitable constant (cf. Riley, 1946). However, such an assumption is invalid during much of the day in tropical seas or during summer days at higher latitudes. Near the surface of the ocean the light intensity will then exceed the proportionality maximum of some 0.15 ly./min. (Section II) so that the greatest productivity will occur at several metres depth and not at the surface. A decrease in the surface illumination will increase rather than decrease the rate of photosynthesis in the surface layers and therefore the net decrease of productivity in the euphotic zone is not necessarily proportional to a decrease in I_s. In examples (Nielsen, 1954, 1955) has shown that a decrease in I_s to a third of its maximum value would decrease the productivity to only two-thirds of its former value and that even with a tenth of the surface light the production in the euphotic zone would only drop to a quarter of its maximum.

The principles behind such calculations are simple. One only has to know the relative photosynthetic rates at various light intensities (for example, the curves given by Ryther, 1956; Nielsen 1937; Nielsen and Al Kholy, 1956) and the actual light intensity at a given depth to compute the relative photosynthetic rate at this depth and thus draw a curve covering a full range of depths in the euphotic zone. From the integral of such curves factors can be evaluated to give the total production rate in the euphotic zone from a knowledge of the rate of photosynthesis at optimum light intensity. These factors will depend upon the surface radiant energy and the light attenuation properties of the water. Ryther (1956) assumed a single extinction coefficient for all photosynthetically active wavelengths and a simple energy–time distribution of sunlight throughout the day. Such an over-simplification is extreme and a more exact treatment is practical without necessitating elaborate experimentation (present author, in preparation). However, several complications arise when attempting to relate photosynthetic rates obtained in a ship-board incubator to actual production in nature (cf. Rodhe, 1957; Nielsen, 1952b, 1954; Verduin, 1957; Cushing, 1957; Doty and Orguri, 1957) and more work is required. The use of comparatively

simple factors or formulae (Nielsen, 1952b; Verduin, 1957) may be all that is justified in the light of present knowledge.

The effect of surface illumination and κ values on total productivity is well treated by Edmondson (1956a) for lakes. In some lakes the standing crop weight is not markedly affected by the depth of the euphotic zone (Verduin, 1956) as there is an inverse correlation between depth and the number of cells per unit volume. A similar relation exists between total production rate and the euphotic depth in tropical waters (cf. Nielsen, 1957). Matters can be complicated by physiological factors, such as the recent observations of daily periodicity in synthesis (Doty and Oguri, 1957; Yentsch and Ryther, 1957; Verduin 1957). Bormann (1956) has noted that the mean intensity of light during the day is not necessarily a good measure of photosynthetic productivity, because for the greater part of the time light energy may be received at an intensity well below the mean.

Section IV: Methods of Measurement

The purpose of this section is to review, briefly, the main techniques that have been used for the measurement of surface and submarine light intensity and the transparency and scattering properties of ocean waters. The description of equipment and instruments is far from complete but should be sufficient to indicate the main types of approach. Details are given of the more common sources of error and practical difficulties that have arisen and the methods used to overcome them.

SURFACE ILLUMINATION AND RADIANT ENERGY

The total solar radiation reaching the ocean surface is measured by its heating effects on a suitably constructed thermopile. The Gier and Dunkle type radiometer, now in commercial production, has the widest spectrum range, but for productivity and many physical studies the ultra-long wavelength radiation is not important and measurements can be made with a pyrheliometer. The instrument manufactured by the Eppley Laboratories at Newport, Rhode Island, is the most commonly used in North America and is received from the makers already calibrated between 0 and 2 ly./min. Ten- or fifty-junction models are available with outputs of around 2 and 8 millivolts per ly./min., respectively. The output is fed to a continuous recording milli-voltmeter. The instrument is sensitive in the wavelength range 3,000 to 50,000 Å. Sources of error in this instrument and methods for reducing these errors have recently been discussed by Fuquay and Buettner (1957). For field use a pocket-type radiation meter has been manufactured by the General Electric Company (type D.W. 60) although this is apparently no longer in production. Less accurate field measurements can be made with various light meters or photographic exposure meters (cf. Nelson and Edmondson, 1955) but these must first be calibrated against a pyrheliometer. It is often convenient to design an integrating circuit for the pyrheliometer or a secondary meter (e.g. W. S. von Arx and R. Walden, quoted by Edmondson, 1956b) so that the total energy over a period of hours or days

can be read directly. Such integration units are now available commercially from the Eppley Laboratories.

The deck measurements of incident radiation that are required to convert submarine readings into vertical extinction coefficients are rarely obtained with a pyrheliometer. A Weston cell or photomultiplier (matching the submarine instrument used) is generally employed, being calibrated before and after a cruise by a standard lamp or against a pyrheliometer. There is much to be said for measuring I_z just under the sea surface (Utterback and Boyle, 1933), so as to bypass the uncertain corrections for surface losses, but practical difficulties arise unless the sea surface is very smooth, and the practice has not been generally adopted.

The calibration of a deck instrument against an artificial light source is only satisfactory if the special characteristics of the source resemble daylight. If a standard lamp of known output (artificial mean sunlight or carbon arc) is used the photocell will subsequently underrate low-angle sky light when it is mounted horizontally on the deck of a ship and a factor of 1.06 should be used to correct for this (Atkins, Clarke *et al.*, 1938).

The output of a deck photometer will generally be proportional to the output of a pyrheliometer, but this is not necessarily the case (Utterback, 1933b) and fluctuations may be recorded by the former that do not show up with the pyrheliometer. The reason for this is associated with the different spectral response of barrier-layer cell photometers as compared with thermopiles, the former having little response in the infra red. The Weston Photronic cell, probably the most widely used on this continent, cuts out above a wavelength of 7,000 Å and when calibrated against a pyrheliometer will record with a sensitivity that is nearly twice as great for a blue sky and obscured sun as when the sun shines on the photocell from a cloudy sky. Thus a series of factors should be used, according to sky conditions, if any worthwhile precision is expected.

If any colour filters are to be used difficulties arise. κ values are not affected, except that the depth at which measurements can be made is reduced. However, the conversion of the output of a photocell into light intensity units presents a problem. The structure of the Eppley pyrheliometer is such that it is difficult to filter the light reaching this instrument. The fraction of the total solar radiation transmitted by a filter on the deck photometer must therefore be computed from the transmission curve of this filter and the spectrum of daylight. The output of a standardized pyrheliometer should be simultaneously compared with that of the photocell on a bright day with either no clouds or a continuous overcast. An annual or bi-annual calibration is probably sufficient.

Vertical extinction coefficients must only be measured when there is bright sunlight and but a few clouds, or when there is a continuous overcast. The sky conditions should always be noted. In no case must a measurement be taken with the sun obscured in an otherwise clear sky. The approximate amounts of direct sunlight and diffuse daylight should be recorded. The latter can be determined by shielding the direct sunlight from the cell by means of a small object held 2 to 3 m. away.

Needless to say the surface of the deck photometer must be kept spotlessly clean and the instrument mounted on gimbals in a position on the superstructure where no appreciable shielding from sun *or skylight* is possible (Poole and Atkins 1937; Atkins, Clarke *et al.*, 1938).

SUBMARINE LIGHT AND VERTICAL EXTINCTION COEFFICIENTS

In many early experiments electron emission-type cells were used, vacuum or gas filled, with sodium, potassium, caesium or caesium–cesium oxide as cathode materials (Atkins and Poole, 1933a; Clarke and Ostler, 1934; Ostler and Clarke, 1935; Poole and Atkins, 1937; subject review by Poole and Atkins, 1928, and Poole, 1936; excellent bibliography of work until 1937 by Atkins, Clarke *et al.*, 1938). The accounts of these early experiments make valuable reading as an introduction to many of the experimental difficulties inherent in all submarine measurements and the methods devised to overcome them. As this type of cell is now rarely if ever used, however, it will not be considered further in the present review. The caesium–cesium oxide cell had some advantage in red light sensitivity but none of these emission cells could be conveniently used at depth; they were relatively difficult to handle, and were less sensitive, as used, than the barrier-type cells that replaced them. The direct use of an underwater thermopile (Birge and Juday, 1929) has not found favour, probably due to technical difficulties and low sensitivity, but one could wish for developments on these lines with modern instrumentation. The photographic recording of submarine light intensity has also not been proven popular because of the complexity of the method and equipment, but has been used by several workers in conjunction with spectrographic equipment (Eriksson, 1933; Lenoble, 1956b, c) and where great sensitivity was required but photomultipliers were not available (Jerlov and Koczy, 1947).

1. General Requirements and Standardization

Although the use of sunlight as a source for the standardization of photocells (see Johnson and Olsson, 1944) is possibly not capable of the precision attainable with a standard lamp and optical bench it has the advantage of simplicity and is sufficiently accurate for most practical purposes. The subject was discussed in the previous section.

Poole and Atkins (1935) describe the use of artificial standards. They favoured a carbon arc, which was more precise than might be expected, and gave a scale agreeing well with the use of mixed daylight. A vacuum tungsten filament standard lamp of colour temperature around 2,350 K° and a candlepower exceeding 50 was found satisfactory with selenium cells. Clarke and Wertheim (1956) used a 30-candlepower Point-o-lite bulb and green filter of known transmission to standardize their photomultiplier. The subject is covered by standard photometry practice but it is worth noting that corrections for the size of source and receiver (cf. Poole and Atkins, 1935) may become important.

No discussion of the many points of instrumental design necessary to ensure the satisfactory sea-going behaviour of a photometer will be attempted here. Reference should be made to original publications for the details of any particular

instrument. There are, however, some points of universal applicability which merit discussion in connection with submarine photometry and the determination of vertical extinction coefficients.

Often the radiation on deck will be so much greater than the linear response limit of the cell that some form of masking is essential. Circular discs with central apertures of various sizes have been employed but a uniformly distributed series of perforations would be preferable and neutral grey glass filters are even better. The output of deck and submarine photometers should be correlated and an interconversion factor found if they are not perfectly matched. When determining κ values the reading of the deck photometer must be taken within a few seconds of the submarine reading and measurements made only when light conditions on deck are constant.

Care should be taken to see that the underwater cell is not in the ship's shadow (Poole, 1936; Poole and Atkins, 1937; Utterback and Jorgensen, 1934). This can be ensured by suspending the photometer from a spar at least 5 m. long, preferably swung from the stern of the boat. Even when direct sunlight is not obscured, however, the ship will mask a considerable fraction of the diffuse skylight. Poole (1936) has estimated the error for a small research vessel with a 2-m. outboard spar to be some 10% at 5 m., 6% at 10 m., decreasing to 2% at 30 m. This applies to diffuse light and the error is greatly reduced when measurements are made on a sunny day.

Several errors can be incurred in submarine photometry from purely optical sources, especially when the output of a deck and submarine photometer are compared. These sources of error are listed and discussed in the excellent review of requirements by Atkins, Clarke *et al.* (1938) and a full discussion is given by Poole (1938). For the reflection losses at interfaces to be equal in both deck and underwater photometers the spaces between glass filter, opals, cover glasses, etc., should be filled with water in both instruments as, in practice, water will almost certainly get into these spaces in the underwater component. The use of cedar oil between these interfaces is worthy of investigation. The very uppermost glass surface of each photometer should be polished. This not only minimizes surface scattering losses but, more important, lessens any changes in these losses that occur when the submarine component is wetted. The reflection losses from these polished surfaces may be high (about 10% for mixed sun and skylight, high-angle sun) but they are nearly equal for both deck and submarine instrument, being a little larger for the former. If a thin layer of water is placed on the surface of the deck photometer in an attempt to equalize air and submarine reflection losses the decrease in reflection thus achieved is compensated for by additional losses (see below), and nothing is gained by the practice. The upper glass surface of deck photometers may be left dry.

Any light with a greater incidence than about 49° will not reach the photosensitive element of a photometer because it will suffer internal reflection from the lower surface of the glass plate used to protect this photo element. The angle of incidence of the light on a horizontal submarine photometer cannot exceed some 49° if the sea is perfectly calm, but when the surface is roughened and

when underwater scattering occurs there is light at all angles entering the instrument. To avoid errors incurred by the failure to record high-incidence light it is now standard practice to use a sheet of opal glass, polished on the upper surface, as the first optical element in any photometer. Filters, and the protective glass enclosing the photocell, go beneath this opal. In the deck cell some 30 to 40% of the light in the opal is scattered back to the glass–air interface. Here much of the light is at such a high incidence that it is internally reflected, but some escapes into the air. If there is a thin layer of water on the glass the amount of light escaping will be appreciably greater (glass–water interface instead of glass–air interface) but most of this will be reflected back again when it subsequently reaches the water–air interface. However, with a deep enough layer of water no such subsequent return is possible and losses from the opal of a submarine cell will exceed those from the opal on a deck cell. Submarine light readings should be multiplied by a factor of 1.09 to allow for this loss, when κ values are calculated from simultaneous deck measurements of I_z.

One final source of error is worth mentioning. Poole (1936) has pointed out that the vertical illumination measured in shallow water, where the sea bottom is light coloured, may be less than is recorded by the photometer. If the water is appreciably turbid, some of the light reflected from the sea bottom is back-scattered into the photometer cell.

2. Barrier Layer Cells

For work in the euphotic zone, i.e. to some 50 to 100 m., the barrier-layer type cell is now almost universally employed, one of the better known being the Western Photronic cell which can be obtained with a wide range of sensitivities and in many mountings. The modern Weston Photronic cell, with a glass cover, responds to light of wavelength between 3,000 and 7,500 Å, with a maximum response around 5,500 Å, and has a linear current output if the external resistance is sufficiently low (less than 200 ohms) when the light intensity exceeds about 10^{-4} ly./min. The limit of sensitivity of these cells depends upon the detection instrument used. With a mechanical pointer type micro-ammeter measurements of some precision can be made of 10^{-4} ly./min. A commercial photometer, deck and submarine components, is made by F. Schueler of Waltham, Massachusetts.

The desirability of making κ measurements with at least three spectral bands has already been stressed. If only a single series of measurements is possible a green filter with a maximum transmission near 5,500 Å should be used. Much of the earlier work was carried out by repeating stations for each colour filter but electromagnetic devices for changing filters have been described (e.g. Utterback and Boyle, 1933; Johnson and Kullenberg, 1946). Typical working details will be found in the papers of Atkins, Clarke, Jerlov, Poole, Utterback, and others quoted earlier in this review. Atkins, Clarke *et al.* (1938) describe a combined vertical extinction coefficient meter and transparency meter, consisting of a horizontal cell looking upward to the sea surface and another cell looking downward to a lamp fixed 1 m. below it.

If productivity experiments are to be made, *in situ*, by ^{14}C or light and

dark bottle measurements, Levring's idea of a central photocell surrounded by a circular frame holding the bottles has much to recommend it, but such equipment is of little use in a rough sea.

Finally mention should be made of the technique described by Atkins, Poole and Warren (1949) where a matched deck cell and submarine cell are wired in opposition. Various opals of known density are placed over the deck and the underwater cell is lowered until a depth is found where a robust microammeter reads zero current. Mean κ values follow from a simple calculation.

If the submarine photometer is used *without any colour filters* the resulting output at any depth is related to the light energy at that depth. The relationship is complex, however, as different wavelengths are filtered out at different depths and the output depends on the spectral response of the photocell. Johnson and Kullenberg (1946) have considered the problem in their interesting paper describing work with a selenium cell. On analysing published data, and a considerable number of unpublished results obtained by Johnson, these authors found that the light attenuation in sea water can be characterized by the *mean transparency of the water between 4,000 and 7,000* Å. If this is known the transparency or κ value at any wavelength in this range can be evaluated with an accuracy comparable with that found experimentally. Johnson and Kullenberg calculated the factor, F, by which the output of a submerged barrier layer cell, without filter, must be multiplied to give the total radiant energy in the range 3,800 to 7,120 Å. This factor was found to depend only on the depth of the measurement and the ratio of u to u_s, the output of submarine and surface photometers, respectively. The authors give a graph showing the value of F as a function of the depth of the submarine cell and the ratio u/u_s. The factor depends little on the sun's angle or cloud conditions and does not vary much from one selenium cell to another. To use these graphs it is only necessary to know the output of the photocell being used for a given solar radiant energy in the visible range. An equally simple procedure makes use of the twelve "typical" water masses defined by Jerlov (1947a). By making a single measurement with a blue or blue-green filter most coastal and oceanic waters may be classified as approximating one of these "typical" waters and thence the total light attenuation with depth can be calculated using the data collected in the Swedish Deep Sea Expedition report. Thus very simple and elegant methods exist for constructing total energy curves in the euphotic zone without the experimental complication of measuring light intensities at many wavelengths. The authors clearly state the approximation involved, including the assumption of constant values in the euphotic zone and the assumption of similar optical properties for all waters of the same mean transparency, but there is little doubt that the uncertainties thus incurred can be neglected in most field experiments designed for productivity studies, unless the water is excessively turbid ($\kappa_{(green)}$ greater than 0.3).

3. Photomultipliers

The sensitivity of a barrier layer cell is such that it cannot be used at a depth greater than 200 m., even at mid-day in the clearest waters. Photomultiplier-type photometers are therefore used for work at greater depths.

These instruments will measure as little as 10^{-12} ly./min. (ca. 10^{-7} of the minimum light measurable by a Weston cell), enabling them to detect illumination at 500 to 600 m. in a clear part of the ocean. Below these depths the light recorded is mainly from the chemiluminescence of the local fauna. The sensitivity of a photomultiplier tube is so great that it becomes an embarrassment in shallow waters during the hours of daylight. The unshielded cell cannot be used with more than 5×10^{-5} ly./min. of radiation and a neutral filter of density 4 is necessary if the instrument is to be used at the surface of the ocean. It is best to have a Weston-type deck cell for recording variations in I_z values when κ is to be measured.

Photomultiplier tubes have a different spectral response from barrier layer cells, being more sensitive to short wavelengths. The peak sensitivity is about 4,500 Å. In deep waters it should only be necessary to use one filter, blue-green, although automatic filter changing equipment has been described (Snodgrass, unpublished). It is general to incorporate automatic depth gauges on these instruments.

Photometers, in which the current output at constant voltage (up to 1,000 v.) is measured, have been described by Clarke and Wertheim (1956), and by Kampa and Bowden (1954) who used an instrument designed by Snodgrass of Scripps Oceanographic Institute. Snodgrass has now designed an improved and more elaborate photometer, although details are not yet published. The instrument described by Hubbard (1956) differs from the above in that the anode current is kept constant. The applied voltage then changes with light intensity in a semi-logarithmic manner (ca. 100 to 1,000 v.).

TRANSPARENCY AND SCATTERING MEASUREMENTS

All transparency meters consist, essentially, of a light source and photocell receiver held a known distance apart (generally 0.5 to 1 m.). Such instruments are described by Pettersson (1934, 1935); Atkins, Clarke *et al.* (1938); Young (1939); Johnson (1944); Joseph (1949, 1950); and Jones and Wills (1956). Bands of turbidity are sometimes less than 1 m. thick so it is better to have the light source and receiver in a horizontal, rather than vertical, plane (cf. Pettersson, 1935). The meters are often calibrated in the laboratory by placing them in turbid waters that have previously been measured for κ° in a long-cell spectrophotometer. Neutral grey standard density wedges have also been used for calibration purposes. No calibration is needed when the instrument is used to detect relative changes of turbidity with depth. Absolute turbidity values are rarely important in productivity studies as the (approximate) κ° values thus measured cannot be used to predict the attenuation of solar radiation with any accuracy. The main value of the instrument is to detect detrital layers where regeneration processes are most active. Williams (1955) has described the construction of a very precise hydrophotometer, a development of his dual filter hydrophotometer reported in 1953. The light is collimated by a honeycomb collimator in front of the photocell and thus only the attenuation of parallel light is measured (true κ° values), all scattered light being eliminated. Recently

Jerlov (1957) has described a meter with a multiple reflection light path of up to 10 m. or more total length which can be used in comparatively clear waters. For most purposes, however, it is doubtful if such precision is necessary. Commercial instruments are obtainable from Askania Werke A.G., Berlin, and Hydrowerkstätten Feinmechanik und Apparatebau G. m. B.H., Kiel. They can be used to a depth of 100 m. with adjustable path lengths and have filters for red and blue light.

Methods for measuring scattered radiation are described by the authors referred to in Section III. The measurement of scattered radiation by a specially designed "scatter meter" is described by Pettersson (1935). The back-scattered radiation from a powerful beam of light pointing down into the water was picked up by a photocell placed in the plane of the lamp. Burt (1955b) describes the use of a Beckman DU spectrophotometer and 50-cm. cells for turbidity measurements on water samples pumped from the sea at various depths. From the results approximate values for the size distribution and number of particles in the water can be calculated. A very sensitive laboratory apparatus is described by Jerlov (1947b).

USE OF THE SECCHI DISC

The secchi disc and its method of use are too well known to need description here, neither is it proposed to discuss the experimental results obtained in various seas. However, in many sea areas secchi disc observations are the only data available and it is of interest to decide what significance these data may have in productivity studies.

The disc depth undoubtedly gives a rough measure of κ in the top 2.5 to 25 m. of water, although the spectral range is extremely wide and the resulting extinction coefficients are very approximate. It will be remembered that the back-scattered illumination in the sea is approximately 2 to 3% of the downward illumination at any depth. An observer looking vertically down into the sea at the surface will see, if he is not confused by surface reflections, a general background illumination of the order of 0.02 to 0.03 I_s. The disc, which ideally should reflect back all the illumination I at depth D will appear to be illuminated at an intensity $I_s \times 10^{-\kappa(2D)}$ as the light has travelled a distance $2D$ from the surface to the disc and back again to the observer's eye. As this illumination will be approximately equal to the background, 0.02 to 0.03 I_s, when the disc vanishes it follows that:

$$0.03 \quad I_s \text{ or } 0.02 \; I_s = I_s \times 10^{-\kappa(2D)}$$

whence:

$$\kappa = \frac{0.75}{D} \text{ or } \frac{0.85}{D} \tag{5}$$

where D is the secchi depth. The approximations used in this derivation do not have to be stressed. Clearly the back-scattering by the water can vary at least between 2 and 5% according to the nature of the suspended material. This alone could involve errors in κ of 25% or more. The reflectivity of the disc will

be appreciably less than unity. Light attenuation occurs mainly by scattering but the absorption contribution cannot be neglected and this introduces subjective factors of disc colour which can greatly affect D in "coloured" coastal or lake waters. Nevertheless, the above relation seems to hold reasonably well in clear ocean waters or at inshore areas where the sea is not excessively coloured or turbid. A factor of 0.75 (1.7 when k is used) was found to apply in the English Channel (Poole and Atkins, 1929), although marked variations are reported (Gall 1949). Riley (1956) found that the approximate κ° value measured on board ship using a Klett red filter No. 66 was related to k estimated from secchi disc by an expression of the form:

$$k = 0.96\, k^\circ_{\text{red}} + 0.246 \tag{6}$$

Empirical relations between secchi depth and κ values of the form:

$$\kappa = \frac{a}{D^b} \tag{7}$$

have been applied with some success (see for example Hanaoka, 1957); b is near 0.7 and a varies from water mass to water mass.

Jones and Wills (1956), studying the waters around Plymouth and the mouth of the Thames obtained a relation:

$$\kappa^\circ = \frac{2.06 \pm 0.035}{D^{(1{\cdot}04 \pm 0{\cdot}02)}} \tag{8}$$

for D values between 0.75 and 21 m., where κ° is the Lambert Law constant found with a transparency meter. If very turbid waters were excluded the relationship was close to:

$$\kappa^\circ = \frac{1.9}{D} \tag{9}$$

indicating that vertical extinction coefficients are some 40% of the true Lambert Law constants. Nan'niti (1953) has treated secchi disc visibility in a highly mathematical paper where both scattering and absorption are considered. The maximum depth in pure water, where only molecular scattering occurs, is theoretically 173 m. The maximum observed in practice is around 60 m.

Jenkins and Bowen (1946) compared the observations of secchi depth and the night visibility of a 1,000-watt light bulb. The latter was consistently visible at about twice the secchi disc depth until offshore waters were reached when the light attenuation from true absorption became about equal to that resulting from scatter. Under these conditions the 1,000-watt light could be seen at some three times the secchi depth (160 m. as against 50 m.).

The relationship between plankton population and secchi disc readings has been discussed, amongst others, by Atkins, Jenkins and Warren (1954), Edmondson (1956a) and Verduin (1956). If the euphotic depth is taken as the depth where I is 1% of I_s (a not unreasonable rough approximation) this should be about 2.5 times the secchi disc depth. A value of 3 was used by Riley (1941) but factors as high as 4 to 5 have been reported for lakes. Although the daily

photosynthesis per unit of crop is doubtless roughly proportional to D, the standing crop per unit volume has been found to be an inverse function of this depth (Verduin, 1956; Atkins, Jenkins and Warren, 1954). Recently Hanaoka (1957) has proposed relatively complex relationships between organic production, fish population, etc., and the light attenuation of the water derived from secchi measurements.

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